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# THE NORTH AMERICAN PHENACODONTIDAE (MAMMALIA, CONDYLARTHRA)

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# THE
# NORTH AMERICAN PHENACODONTIDAE (MAMMALIA, CONDYLARTHRA)

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## Abstract

The condylarth family Phenacodontidae is composed of five genera, *Desmatoclaenus, Tetraclaenodon, Phenacodus, Prosthecion* and *Ectocion,* and ranges from late Puercan (early Paleocene) to Bridgerian (middle Eocene) in North America. The European record includes two genera, *Phenacodus* and *Almogaver,* ranging from Sparnacian (early Eocene) to Lutetian (middle Eocene). Of these, North American *Phenacodus* and *Ectocion* are represented by multiple species. Numerical treatment of over 2,800 specimens confirms the species diversity and permits a reduction in the number of valid species. Various evolutionary trends developed which permitted better resource utilization, but the phenacodonts ultimately were forced to extinction by the more efficient perissodactyls.

## Introduction

Among the most common mammals in collections from North American localities of middle Paleocene through early Eocene age are representatives of the condylarth family Phenacodontidae. Although they are prominent parts of most assemblages and were described early in the study of each assemblage, distinctions and relationships between the various genera and species have been unclear. These difficulties have been noted by several authors (Granger, 1915; Dorr, 1958; Schiebout, 1974), but no comprehensive attempt at clarification of the family has been made previously.

This study presents a revised taxonomy of the Phenacodontidae based upon direct study and measurement of over 2,800 specimens and a careful literature survey. Large samples from numerous localities have been assembled, permitting statistical approaches to be utilized.

The majority of phenacodont specimens are maxillary and mandibular fragments including partial dentitions. Many species are known only from teeth, and the systematics of the family are based on dental characteristics. Some evolution can be seen in the postcranium, such as the feet (Radinsky, 1966), but because of the scarcity of associated postcranial material these are of no value at the species level.

Tooth measurements utilized are the standard dimensions recorded on mammalian teeth: maximum length for both upper and lower teeth, maximum width on upper and lower premolariform teeth and both widths on molariform teeth. These measurements were taken with micrometer calipers and rounded to the nearest 0.1 mm. All measurements were taken by the writer.

Phenacodonts in the following collections were examined directly: Princeton University; The American Museum of Natural History; Yale University Peabody Museum; Museum of Comparative Zoology, Harvard University; Field Museum of Natural History; Carnegie Museum; United States National Museum; Pratt Museum, Amherst College; Museum of Paleontology, University of California, Berkeley; University of Wyoming Geology Museum; University of Michigan Museum of Paleontology.

## Abbreviations

| | |
|---|---|
| AMNH | - American Museum of Natural History, New York |
| PU | - Princeton University |
| USNM | - U.S. National Museum of Natural History, Smithsonian Institution |
| UMMP | - University of Michigan Museum of Paleontology |
| CM | - Carnegie Museum of Natural History |
| AC | - Pratt Museum, Amherst College |
| FMNH | - Field Museum of Natural History, Chicago |
| N | - number of specimens |
| X | - mean |
| s | - standard deviation |
| CV | - coefficient of variation |
| O.R. | - observed range |
| W | - maximum width of tooth |
| $W_{ant}$ | - width across anterior part of tooth |
| $W_{post}$ | - width across posterior part of tooth |
| L | - maximum length of tooth |

## Acknowledgments

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## Statistical Treatment

A recent study by Gingerich (1974) illustrated the utility of particular dental measurements in verifying distinctions between closely related species. Gingerich was concerned with differentiating sympatric species of primates, but his methodologies are of general applicability. Numerical approaches are especially valuable in determining the presence of sympatric species at single localities, as well as for demonstrating probable synonymies.

Various means of representing numerical data on phenacodont teeth are employed below as permitted by the availability of data. The simplest is tabulation of the measurements of large and/or particularly important samples and calculation of basic statistical parameters (standard deviation and coefficient of variation). As has been presumed by countless paleontologists, and documented by Gingerich (1974), the first and second molars show the lowest coefficients of variation and are therefore the most useful teeth for comparisons of samples. Therefore, bivariate plots of length versus width for these teeth are presented; polymodality within these plots is then suggestive of multiple species. A third and more readily visualized projection of these data is one using a single axis paralleling the main axis of the bivariate plot. The unit employed here is that used by Gingerich (1974), the logarithm of the product of tooth length multiplied by tooth width for the first lower molar. The use of the logarithm in this plot removes the effect of size on variability and provides a more clear representation of the individual groupings.

## History of Study of Phenocodontidae

The phenacodont condylarths are based upon the common late Paleocene and early Eocene genus *Phenacodus;* the initial description (Cope, 1873) was of an isolated $M_3$ of *P. primaevus* from the conglomeratic facies of the Wasatch formation near Evanston, Wyoming. In 1874 Cope named *P. sulcatus* on a peculiar $M^3$ which later proved so indeterminate that the name is best abandoned as a *nomen nudum* (Granger, 1915, p. 347). In the same 1874 paper Cope described *P. omnivorous* on a $M^3$ from the early Eocene of northern New Mexico. That specimen was placed into *P. primaevus* by Granger, 1915. *Opisthotomus astutus* (Cope, 1875) is based on an isolated lower molar from the New Mexico Eocene; the holotype has since been lost, but Granger (1915) thought it was probably *Phenacodus brachypternus*. Another species, *O. flagrans,* was described in the same paper; that lower molar also is lost. Granger (1915) thought it might be a milk tooth of a *P. primaevus*.

In 1880 Cope described (as *Hyracotherium*) *P. vortmani* on a left dentary with $P_4$-$M_1$ from Lost Cabin beds along Alkali Creek in the Wind River Basin of Wyoming. In 1881 Cope described *P. trilobatus* from the lower "Wasatch" of the Bighorn Basin of Wyoming. Granger (1915) placed this into synonymy with *P. primaevus. P. apternus* was described by Cope in 1882 (1882c, p. 180); this later was synonymized with *P. vortmani* (Granger, 1915). Also in 1882 Cope described the smallest recognized species of *Phenacodus, P. brachypternus,* from the lower Eocene of the Bighorn Basin. A third 1882 species from the Bighorn Basin early Eocene was *P. hemiconus.* Cope's final contribution was *P. nunienus* (1884, p. 434); this has since proven to be mostly postcranial fragments of *Pachyaena.*

In 1894 Marsh named *Eohyus distans;* this is probably an $M^3$ referable to *P. primaevus* (Granger, 1915).

Since the turn of the century, work on Eocene *Phenacodus* has been devoted largely to sorting out the species mentioned above and allying morphologically useful material with the various types. The first review of *Phenacodus* (Granger, 1915) used the American Museum of Natural History collection, which by then included most of Cope's materials. Granger retained Cope's *P. primaevus* and incorporated into it *P. omnivorus, P. trilobatus, P. nunienus, E. distans,* and possibly also *O. flagrans.* He differentiated several subspecies of *P. primaevus,* including *P. p. hemiconus,* based on Cope's species, and *P. p. robustus* for a few large specimens. In addition he separated *P. copei* from *P. vortmani* on a minor size difference, and introduced the moderate sized *P. intermedius.* Granger retained both *P. brachypternus* and *P. astutus* at the small end of the *Phenacodus* size spectrum.

The first Paleocene true *Phenacodus* was mentioned by Gidley (1917, p. 59) from the Mason Pocket, Ignacio, Colorado. Granger (1917, p. 827) also commented on this material, but it was not until 1935 that Simpson described two small species, *P. matthewi* and *P. gidleyi,* and one larger species, *P. grangeri,* from this type area for the Tiffanian.

In 1937 Simpson reviewed the Clark Fork Fauna (see Wood, 1966) and modified Granger's 1915 treatment of *Phenacodus*. He separated the few large specimens as *P. robustus*, elevating Granger's subspecies to full specific rank, and reduced *P. intermedius* to the rank of subspecies along with *P. p. hemiconus* and *P. p. primaevus*.

Gazin (1942), working with a late Paleocene fauna from along the western side of the Green River Basin, Wyoming, named the medium-sized *P. almiensis*. In 1956 he described another early Tiffanian *Phenacodus, P. bisonensis* from Bison Basin in central Wyoming.

In 1958 Dorr described *Tetraclaenodon transitus* from the Battle Mountain local fauna of the Hoback formation in the Hoback Basin of western Wyoming.

McKenna in 1960 extended *P. matthewi* into the earliest Wasatchian by claiming its presence in the Four Mile local fauna of northern Colorado. Guthrie (1967), working with material from the Lysite member of the Wind River formation, reunited Granger's *P. copei* with Cope's *P. vortmani*. Delson (1971, p. 346) reassigned the material regarded as *P. matthewi* by McKenna (1960) to *P. vortmani* and suggested the synonymy of *P. matthewi* and *P. gidleyi* from Ignacio. West in West and Atkins (1970) extended the range of *P. primaevus* into the middle Eocene at Tabernacle Butte, Wyoming.

*Tetraclaenodon* was also initially recognized by Cope (1881, p. 492), who called it *Phenacodus puercensis*. On the same page he described *Protogonia subquadrata* and in 1882 (1882b, p. 833) named a second species of *Protogonia, P. pliciferus*. In 1883 (p. 561) Cope named another species of middle Paleocene *Phenacodus, P. calceolatus*. In 1888 (p. 359) he referred the holotype of *Protogonia subquadrata* to the species *puercensis* which he transferred to *Protogonia* from *Phenacodus*. Also in 1888 (p. 330) Cope named *Mioclaenus floverianus* and *Protogonia zuniensis*.

Scott (1892, p. 499) removed *M. floverianus* to a new genus, *Tetraclaenodon*. In an 1897 review, Matthew synonymized Cope's *Euprotogonia* (the new generic name replaced *Protogonia* which Cope erroneously thought was preoccupied) with Scott's *Tetraclaenodon*. Although it was technically invalid, *Tetraclaenodon* became the commonly used name; this situation was formalized after a 1970 petition to the International Commission on Zoological Nomenclature (West and Baird, 1970).

Matthew also named a new species in 1897, assigning two specimens which Cope had referred to *Euprotogonia zuniensis* to the new species *E. minor*. The type of *E. zuniensis* proved to be identical to the arctocyonid *Tricentes subtrigonus*.

Northward extension of *Tetraclaenodon* occurred with the discovery of middle Paleocene localities in the Crazy Mountain Field of Montana (Douglass, 1902) and in western North Dakota (Lloyd and Hares, 1915). Simpson (1935b, 1937a) studied the Crazy Mountain Field fauna, naming a new small species *T. symbolicus.*

The most recent review of *Tetraclaenodon,* published posthumously by Matthew (1937) with Simpson's aid, synonymized the species *subquadratus, calceolatus* and *floverianus* into *T. puercensis,* and *minor* into *T. plicifera* (p. 188).

Additional collecting and the discovery of new middle Paleocene localities such as Rock Bench Quarry (Jepsen, 1930, 1940), Paskapoo (Russell, 1958), and Goler (West, 1970) have expanded the geographic and temporal but not the taxonomic range of *Tetraclaenodon.*

The physically smallest genus of phenacodonts is *Ectocion.* It was initially recognized by Cope (1882c, p. 182) as *Oligotomus osbornianus;* later that year (1882a, p. 522) the generic name was changed to *Ectocion* and in 1884 (p. 696) the gender of the specific name was corrected to *osbornianum.*

This genus was included in Granger's 1915 phenacodont review; he described a new small species, *E. parvus* from the "Clark Fork" of Big Sand Coulee, Bighorn Basin, a new large species, *E. superstes,* from the Wind River Basin Lost Cabin, and a new species only slightly smaller than *E. osbornianum, E. ralstonensis,* also from the "Clark Fork" of Big Sand Coulee.

In 1929 L. Russell described *E. collinus* on an $M^3$ from the Paskapoo late Paleocene near Calgary, Alberta.

Simpson's study (1935b, 1937a) of the Paleocene faunas of the Crazy Mountain area, Montana, resulted in a new genus, *Gidleyina,* somewhat more primitive dentally than *Ectocion,* with three species: *G. montanensis, G. silberlingi* and *G. superior.* Also in 1937, in his review of the Clark Fork fauna, Simpson reduced Granger's *E. ralstonensis* to a subspecies of *E. osbornianum.* In 1943 Simpson used *Ectocion* as an example in a discussion of chronoclines. All late Paleocene and early Eocene material was placed in *E. osbornianum* with four successive subspecies: *E. o. ralstonensis* (Clark Fork); *E. o. complens* (Sand Coulee); *E. o. osbornianum* (Graybull); *E. o. superstes* (Lost Cabin).

Gazin (1956a, p. 42) added another species, *G. wyomingensis,* from the Bison Basin early Tiffanian.

McKenna (1960, p. 103) disagreed with Simpson's 1934 scheme of *Ectocion* classification and proposed the following arrangement: Paskapoo — *E. collinus;* Clark Fork — *E. parvus* and *E. ralstonensis;* Sand Coulee — *E. o. complens;* Graybull — *E. o. osbornianum;* Lysite — no *Ectocion;* Lost Cabin — *E. superstes.* He added the comment that *E. collinus* and *E. superstes* might not actually be *Ectocion.*

Delson (1971, pp. 347-8) advocated elimination of the subspecies, placed most specimens from the Eocene into *E. osbornianum*, tentatively retained *E. superstes*, and speculated that *E. parvus* might belong in *Hyopsodus*.

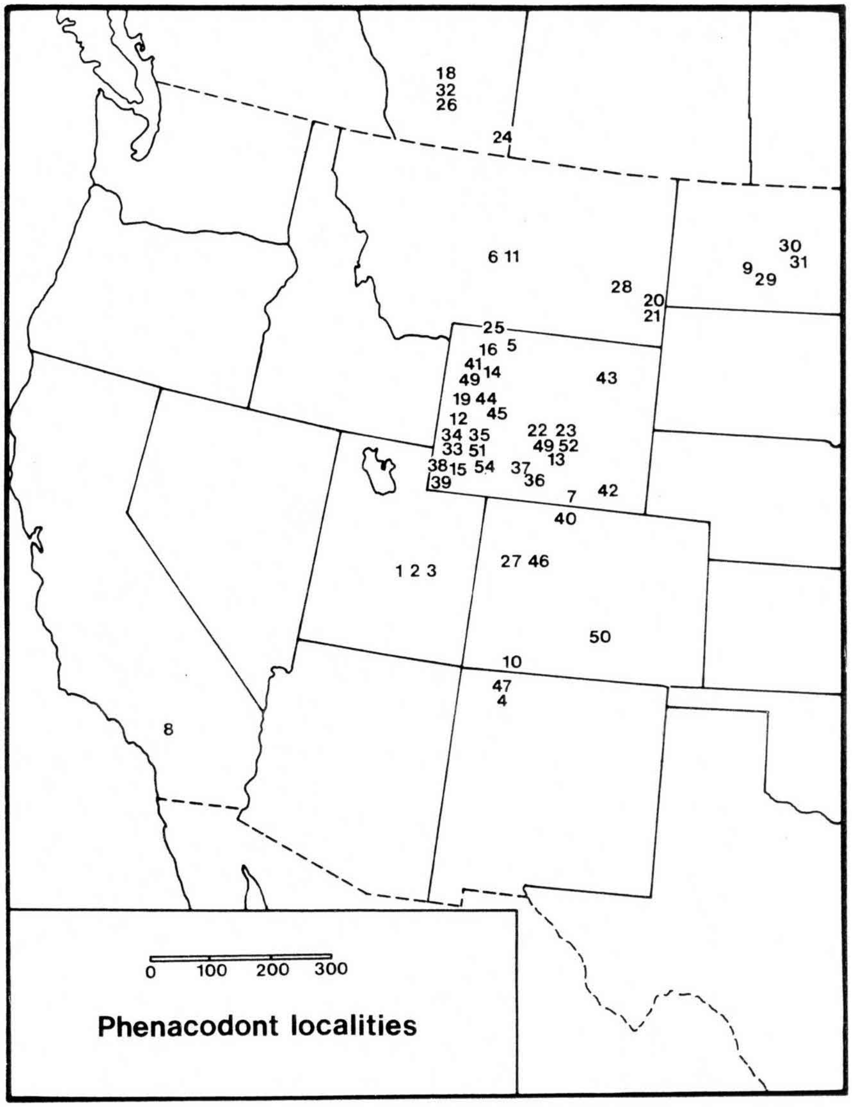


**Figure 1.** North American localities at which phenacodont condylarths have been found. Locality data, taxa recovered, and reference are given in Table 1.

# Table 1. Phenacodont Localities

| Locality | Age | Formation | Taxa | Reference |
|---|---|---|---|---|
| 1. Dragon Canyon | late Puercan | North Horn | **D. hermaeus* | Gazin, 1941 |
| 2. Dragon Canyon | early Torrejonian | North Horn | *D. hermaeus* | Gazin, 1941 |
| 3. Flagstaff Peak | Puercan | North Horn | *D. hermaeus* | Spieker, 1960 |
| 4. San Juan (several levels) | Torrejonian | Nacimiento | **T. puercensis* | Matthew, 1937 |
| 5. Rock Bench Quarry | Torrejonian | Ft. Union | *T. puercensis* | Jepsen, 1940 |
| 6. Crazy Mountain (several levels) | Torrejonian | Lebo | *T. puercensis* | Simpson, 1937a |
| 7. Swain Quarry | Torrejonian | Ft. Union | *T. puercensis* | AMNH locality |
| 8. Laudate | Torrejonian | Goler | *T. puercensis* | West, 1970 |
| 9. Heart River | Torrejonian | Ft. Union | *T. puercensis* | West, 1970 |
| 10. Mason Pocket | Tiffanian | Tiffany | **P. grangeri*<br>*P. matthewi* | Simpson, 1935a |
| 11. Crazy Mountain (several levels) | Tiffanian | Melville | *T. puercensis*<br>**E. montanensis* | Simpson, 1937a |
| 12. Battle Mountain | Tiffanian | Hoback | *P. grangeri*<br>*E. wyomingensis* | Dorr, 1958 |
| 13. Bison Basin (several levels) | Tiffanian | Ft. Union | *P. bisonensis*<br>*E. wyomingensis*<br>*P. grangeri* | Gazin, 1956a |
| 14. Cedar Point Quarry | Tiffanian | Ft. Union | *P. grangeri*<br>*P. bisonensis*<br>*E. wyomingensis* | Princeton locality |
| 15. Twin Creeks | Tiffanian | Evanston | *E. wyomingensis*<br>*P. primaevus* | Gazin, 1956c |
| 16. Polecat Bench (several levels) | Tiffanian | Ft. Union | *P. primaevus*<br>*P. vortmani*<br>*E. osbornianum* | Jepsen, 1940, Jepsen and Woodburne, 1969, and unpublished Princeton localities |
| 17. Big Bend | Tiffanian | Black Peaks | *P. grangeri*<br>*P. matthewi*<br>*E. montanensis* | Schiebout, 1974 |
| 18. Elbow River | Tiffanian | Paskapoo | *T. puercensis* | Russell, 1958 |
| 19. Love Quarry | Tiffanian | Hoback | *P.* sp. | McKenna, 1972 |
| 20. 7-Up Butte | Tiffanian | Ft. Union | *P. grangeri* | Princeton locality |
| 21. White Site | Tiffanian | Tongue River | *P. grangeri* | Princeton locality |
| 22. Shotgun Butte | Tiffanian | Ft. Union | *E. osbornianum*<br>*P. primaevus* | Russell, 1967 |
| 23. Badwater-Malcolm's Locality | Tiffanian | Ft. Union | *P. primaevus*<br>*E. osbornianum*<br>*P.* sp. | Krishtalka, Black and Riedel, 1975 |
| 24. Cypress Hills | Tiffanian | Ravenscrag | *E. osbornianum* | Krishtalka, 1973 |
| 25. Bear Creek | Tiffanian | Ft. Union | *P. primaevus* | Simpson, 1929 |
| 26. Erickson's Landing | Tiffanian | Paskapoo | *P.* sp. | Simpson, 1927 |
| 27. DeBeque | Tiffanian | DeBeque | *Prosthecion major* | Patterson and West, 1973 |
| 28. Circle | Tiffanian | Tongue River | *E.* sp. | Wolberg, pers. comm. |
| 29. Judson | Tiffanian | Tongue River | *P. primaevus* | Holtzman, pers. comm. |
| 30. Riverdale | Tiffanian | Tongue River | *E. wyomingensis*<br>*P. primaevus* | Holtzman, pers. comm. |
| 31. Brisbane | Tiffanian | Tongue River | *E. wyomingensis* | Holtzman, pers. comm. |

| | | | | |
|---|---|---|---|---|
| 32. Cochrane | late Tiffanian | Paskapoo | *P. vortmani* | Russell, 1958 |
| 33. Buckman Hollow | late Tiffanian | Almy | *P. primaevus*<br>*P. vortmani*<br>*E. osbornianum* | Gazin, 1956b |
| 34. UM-Sub-Wyo-10 | Tiffanian | Hoback | *P. copei* | Dorr, 1958 |
| 35. UM-Sub-Wyo-20 | Tiffanian | Hoback | *P. primaevus* | Dorr, 1958 |
| 36. Bitter Creek | early Wasatchian | Wasatch | *P. primaevus* | Gazin, 1962; Savage, pers. comm. |
| 37. Red Desert | early Wasatchian | Wasatch | *P. brachypternus* | Gazin, 1962 |
| 38. Elk Mountain | early Wasatchian | Wasatch | *P. vortmani* | Gazin, 1962 |
| 39. Knight Station | early Wasatchian | Wasatch | *P. primaevus* | Gazin, 1962 |
| 40. Four Mile | early Wasatchian | Wasatch | *P. primaevus*<br>*P. vortmani*<br>*P. brachypternus*<br>*E. osbornianum* | McKenna, 1960 |
| 41. Bighorn Basin | early Wasatchian | Willwood | *P. primaevus*<br>*P. vortmani*<br>*P. brachypternus*<br>*E. osbornianum*<br>*E. parvus* | Granger, 1915 |
| 42. Cooper Creek | early Wasatchian | Wind River | *P. primaevus* | Prichinello, 1971 |
| 43. Powder River | early Wasatchian | Wasatch | *P. primaevus*<br>*P. vortmani*<br>*P. brachypternus*<br>*E. osbornianum* | Delson, 1971 |
| 44. Lower variegated | early Wasatchian | ? | *P. primaevus*<br>*P. vortmani*<br>*P. brachypternus*<br>*E. osbornianum*<br>*E. ?parvus* | McKenna, 1972 |
| 45. Buckskin Ridge | Wasatchian | ? | *P.* sp. | McKenna, 1972 |
| 46. DeBeque | Wasatchian | DeBeque | *P. primaevus*<br>*E. osbornianum*<br>*E. ?parvus* | Patterson, B., 1936 unpublished material |
| 47. San Jose | Wasatchian | San Jose | *P. primaevus*<br>*P. vortmani*<br>*P. brachypternus* | Granger, 1915 |
| 48. Lysite | middle Wasatchian | Wind River | *P. brachypternus*<br>*P. vortmani* | Guthrie, 1967 |
| 49. Bighorn Basin | middle Wasatchian | Willwood | *P. vortmani* | Granger, 1915 |
| 50. Huerfano | late Wasatchian | Huerfano | *P. vortmani* | Robinson, 1966 |
| 51. New Fork-Big Sandy | late Wasatchian | Wasatch | *P. vortmani*<br>*P. primaevus* | West, 1973 |
| 52. Lost Cabin | late Wasatchian | Wind River | *P. vortmani*<br>*P. primaevus*<br>*E. superstes* | Guthrie, 1971 |
| 53. Oil House | Wasatchian | Hannold Hill | *P. primaevus* | Wilson, 1967 |
| 54. Tabernacle Butte | Bridgerian | Bridger | *P. primaevus* | West and Atkins, 1970 |

**D.* — *Desmatoclaenus*
*T.* — *Tetraclaenodon*
*P.* — *Phenacodus*
*E.* — *Ectocion*

West (1971) suggested, but did not substantiate, the inclusion of *Gidleyina* in *Ectocion;* this is further discussed below.

Both *Desmatoclaenus* and *Prosthecion* are known from very small samples. *Desmatoclaenus* (Gazin, 1941) is known from two described species, *D. hermaeus* and *D. paracreodus,* from the late Puercan — early Torrejonian beds of east-central Utah. *Prosthecion major* (Patterson and West, 1973), the only species of that genus, was collected by Patterson in the DeBeque formation of western Colorado. Neither of these genera is known from additional areas.

Figure 1 shows the North American localities from which phenacodont materials have been collected.

## Revised Systematics

The following genera and species of North American Phenacodontidae are regarded as valid and discussed below:

*Desmatoclaenus hermaeus*
*Tetraclaenodon puercensis*
*Phenacodus matthewi*
*Phenacodus bisonensis*
*Phenacodus grangeri*
*Phenacodus brachypternus*
*Phenacodus vortmani*
*Phenacodus primaevus*
*Prosthecion major*
*Ectocion montanensis*
*Ectocion wyomingensis*
*Ectocion osbornianum*
*Ectocion parvus*
*Ectocion superstes*

Individual specimens and samples of phenacodonts have been described in great detail by many authors. Therefore, additional description is redundant and serves no useful purpose, so will be avoided and reference made to the appropriate papers. Diagnoses for all species considered valid will be included below.

## ORDER CONDYLARTHRA
## FAMILY PHENACODONTIDAE COPE, 1881
### *DESMATOCLAENUS* Gazin, 1941

*Desmatoclaenus* Gazin, 1941, Proc. U.S. Nat. Mus., v. 91, p. 34.

**Type species;** *Desmatoclaenus hermaeus* Gazin, 1941, Joe's Valley member, North Horn formation, late early Paleocene and early middle Paleocene, central Utah.

**Included species:** Type only.

**Range:** Late early Paleocene and early middle Paleocene.

**Distribution:** Central Utah.

**Revised diagnosis**: Simple $P^3$; $P^4$ with low, independent parastyle, no intermediate conules; upper molars lack mesostyle, cingulum discontinuous internally, small hypocone and intermediate conules; $M^1$ square; $M^2$ wide with prominent parastyle; $M^3$ small with poorly developed metacone and no hypocone, parastyle smaller than in anterior molars. $P_3$ linear with low anterior cusp; $P_4$ with distinct low paraconid, large protoconid and closely associated metaconid, talonid with well developed hypoconid and small entoconid; lower molars with well developed lingually situated paraconids and distinct trigonid basin, as in *Protogonodon*, and small anterior cingulum; $M_3$ relatively small with cuspidate entoconid-hypoconulid crest.

### *Desmatoclaenus hermaeus* Gazin, 1941
(Figure 2; Table 2)

*Desmatoclaenus hermaeus* Gazin, 1941, Proc. U.S. Nat. Mus., v. 91, p. 34.

*Desmatoclaenus paracreodus* Gazin, 1941, Proc. U.S. Nat. Mus., v. 91, p. 37.

**Holotype:** U.S.N.M. 16202, Wagonroad level, Joe's Valley Member, North Horn formation, early middle Paleocene, Dragon Canyon, Central Utah.

**Range**: Late early Paleocene and early middle Paleocene.

**Distribution**: Central Utah.

**Diagnosis**: As for the genus.

**Discussion**: Gazin (1941, pp. 34-39) described two species differentiated by slightly greater size and somewhat more robust teeth in *D. paracreodus* than in *D. hermaeus*. The sample of this genus is so small, ten specimens, that these variations in size (ranging from 7% to 20% on the various dimensions) are readily accommodated in a single species and the morphologic differences are less than those seen in later well-defined phenacodont species. The coefficients of variation (Table 2) are well within the generally accepted limits for a single species. Therefore, it seems reasonable to include all the specimens in *D. hermaeus*.

In an earlier paper (West, 1971, p. 5) I suggested that *Desmatoclaenus* should be synonymized with the much better known Paleocene arctocyonid *Loxolophus* and thus removed from the Phenacodontidae. I no longer hold that view, and now agree with Gazin's conclusion (1941, pp. 36-37) that *Desmatoclaenus* provides a suitable structural intermediate between the Puercan species of the arctocyonid *Protogonodon* and the common Torrejonian phenacodont *Tetraclaenodon*. Several Puercan species of *Protogonodon* are known (Matthew, 1937); a complete review of them will be necessary to adequately assess their probability as phenacodont ancestors.

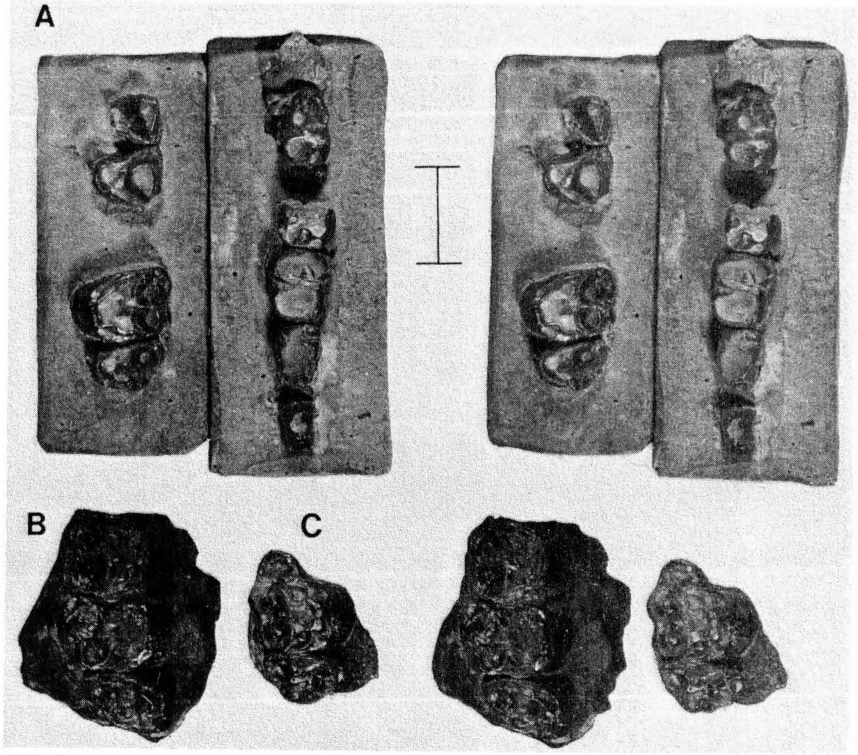


**Figure 2.** *Desmatoclaenus hermaeus,* stereophotographs. A. USNM 16202, holotype, North Horn formation, Dragon Canyon, Utah. Left $P^3$-$P^4$, $M^2$-$M^3$; left $P_3$-$M_3$. B. USNM 16201, North Horn formation, Dragon Canyon, Utah. Right $M^1$-$M^3$. C. USNM 16177, North Horn Formation, Dragon Canyon, Utah. Right $M^2$-$M^3$.
Scale unit represents 1 cm.

## *TETRACLAENODON* Scott, 1892

*Phenacodus* (in part) Cope, 1873, Paleo. Bull, v. 17, p. 3

*Protogonia* Cope, 1881a, Proc. Am. Phil. Soc., v. 19, p. 492.

*Mioclaenus* (in part) Cope, 1881b, Am. Nat., v. 15, p. 830.

*Tetraclaenodon* Scott, 1892, Proc. Acad. Nat. Sci. Phila., v. 44, p. 209.

*Euprotogonia* Cope, 1893 in Earle, 1893, Am. Nat., v. 27, p. 378.

**Type species**: *Tetraclaenodon puercensis* (Cope, 1881), Nacimiento formation, middle Paleocene, San Juan Basin, New Mexico.

**Included species**: Type species only.

**Range**: Middle to early late Paleocene.

**Distribution**: Western North America.

**Diagnosis**: Incisors small, canines large and sharp; anterior premolars simple; $P_3$ with tiny low anterior paraconid, high protoconid, small heel with median ridge; $P_4$ with massive protoconid, distinct paraconid and metaconid, large bicuspid talonid, not so molariform as in *Phenacodus* or *Ectocion*; lower molars with complete paraconid crest and frequently distinct paraconids perched on the anterior flank of metaconid; $M_3$ narrow with paraconid more medial and three-cusped talonid. $P^2$ with small posterior basin; $P^3$ and $P^4$ with prominent protocones, paracone higher than metacone, no hypocone; $P^4$ with small paraconule, occasionally a metaconule, less molariform than in *Phenacodus* and *Ectocion;* molars with prominent conules, weak mesostyle on $M^1$ and $M^2$, hypocone markedly independent and slightly lingual of protocone, $M^3$ small, lacking hypocone and seldom with mesostyle.

### *Tetraclaenodon puercensis* Cope, 1881
(Figures 3-6; Tables 3-5)

*Phenacodus puercensis* Cope, 1881a, Proc. Am. Phil. Soc., v. 19, p. 492.

*Protogonia subquadrata* Cope, 1881a, Proc. Am. Phil. Soc., v. 19, p. 492.

*Protogonia plicifera* Cope, 1882b, Am. Nat. v. 16, p. 833.

*Phenacodus calceolatus* Cope, 1883, Proc. Am. Phil. Soc., v. 20, p. 561.

*Mioclaenus floverianus* Cope, 1888, Trans. Am. Phil. Soc., v. 16, p. 330.

*Protogonia zuniensis* Cope, 1888, Trans. Am. Phil. Soc., v. 16, p. 330.

*Euprotogonia minor* Matthew, 1897, Bull. Am. Mus. Nat. Hist., v. 9, p. 310.

*Tetraclaenodon symbolicus* Gidley in Simpson, 1935b, Proc. U.S. Nat. Mus., v. 83, p. 239.

**Holotype**: AMNH 3832, Nacimiento formation, middle Paleocene, San Juan Basin, New Mexico.

**Range**: Middle Paleocene and early late Paleocene.

**Distribution**: Western North America.

**Diagnosis**: As for the genus.

**Discussion**: *Tetraclaenodon* commonly has been separated into at least two size-dependent species. Current literature usually lists a cosmopolitan large species, *T. puercensis,* a small northern species, *T. symbolicus,* and a small southern species, *T. pliciferus.* Description of the New Mexico material may be found in Matthew

(1937, pp. 187-193), and of Montana material in Simpson (1937a, pp. 246-250).

My examination of *Tetraclaenodon* fails to reveal a clear-cut distinction between a large and a small group. Plots (Figures 5 and 6) of molar dimensions produce the initial impression that there is in-

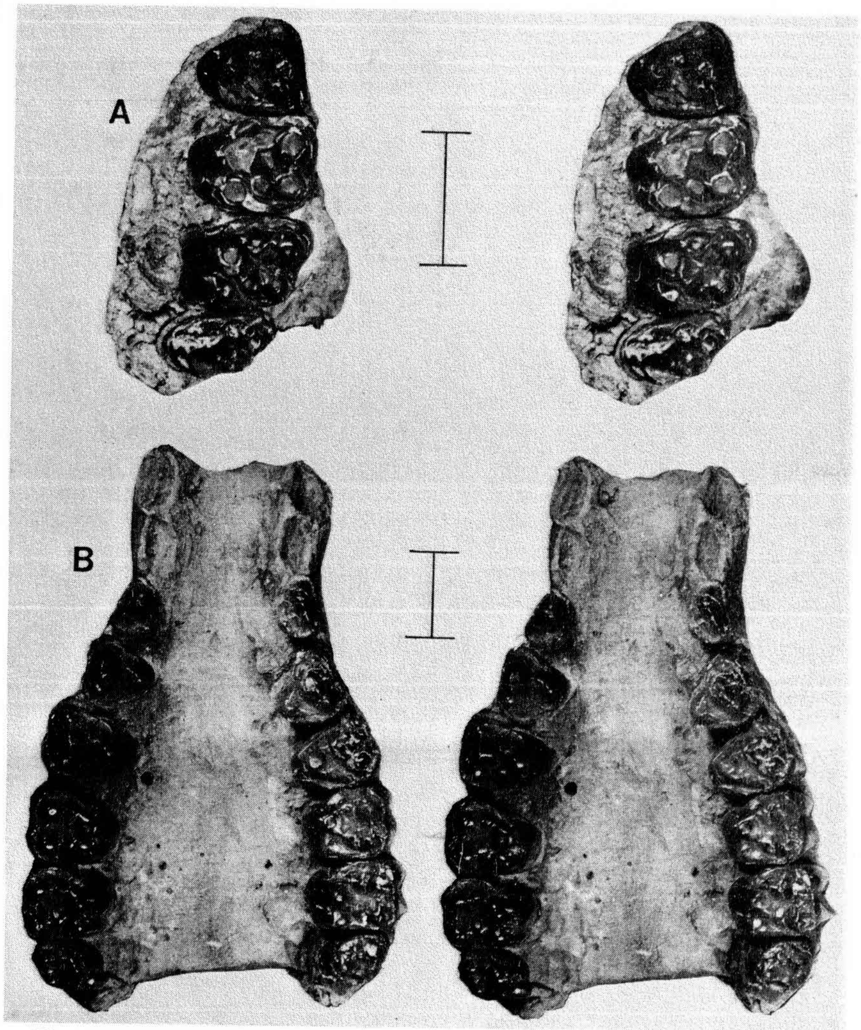


**Figure 3.** *Tetraclaenodon puercensis,* stereophotographs. **A.** AMNH 3937, Nacimiento formation, San Juan Basin, New Mexico. Left $P^4$-$M^3$. **B.** AMNH 16653, Nacimiento formation, San Juan Basin, New Mexico. Right and left $P^2$-$M^3$.
Scale unit represents 1 cm.

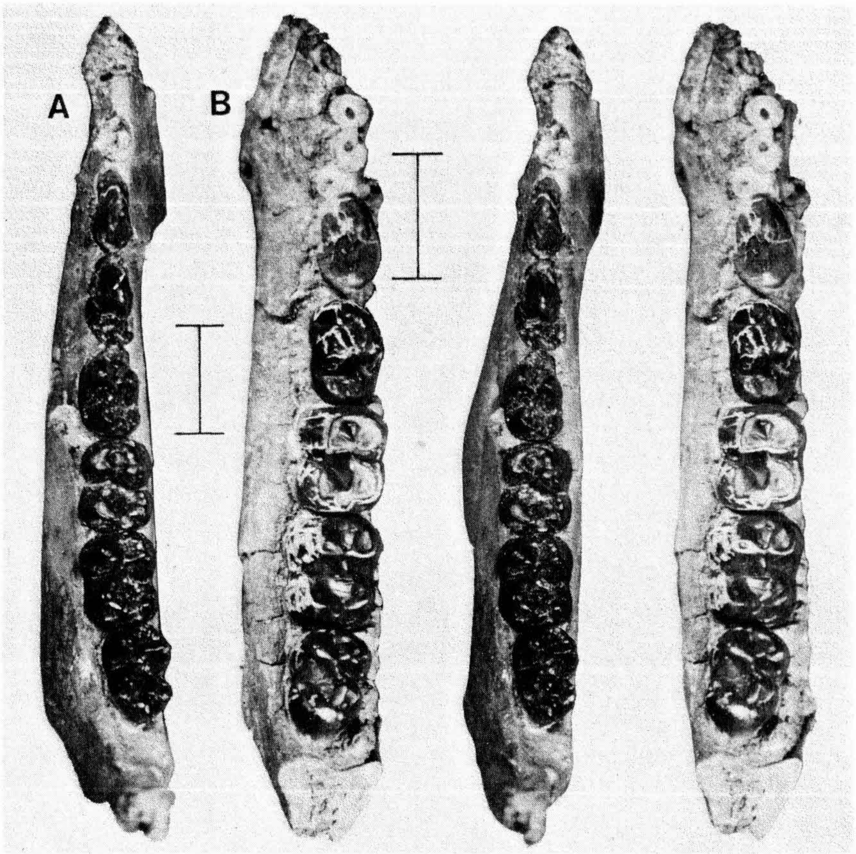


**Figure 4.** *Tetraclaenodon puercensis,* stereophotographs. **A.** PU 13954, Fort Union formation, Rock Bench Quarry, Wyoming. Left $P_2$-$M_3$. **B.** AMNH 15933, Nacimiento formation, San Juan Basin, New Mexico. Right $P_3$-$M_3$.
Scale unit represents 1 cm.

deed a group of a small number of early Torrejonian specimens that are distinctly smaller than other *Tetraclaenodon* materials; furthermore, the slope of a line drawn through that part of the scatter is noticeably less than the slope of a line drawn through the scatter of the large material. However, when the specimens involved in these plots are more closely examined, it is found that teeth from a single jaw fall into both parts of this scatter. This strongly suggests that there is a single variable taxon involved.

When the standard statistical parameters are calculated for samples of *Tetraclaenodon* (Tables 3-5) a peculiar pattern emerges. One sample of *Tetraclaenodon* is restricted geologically — that

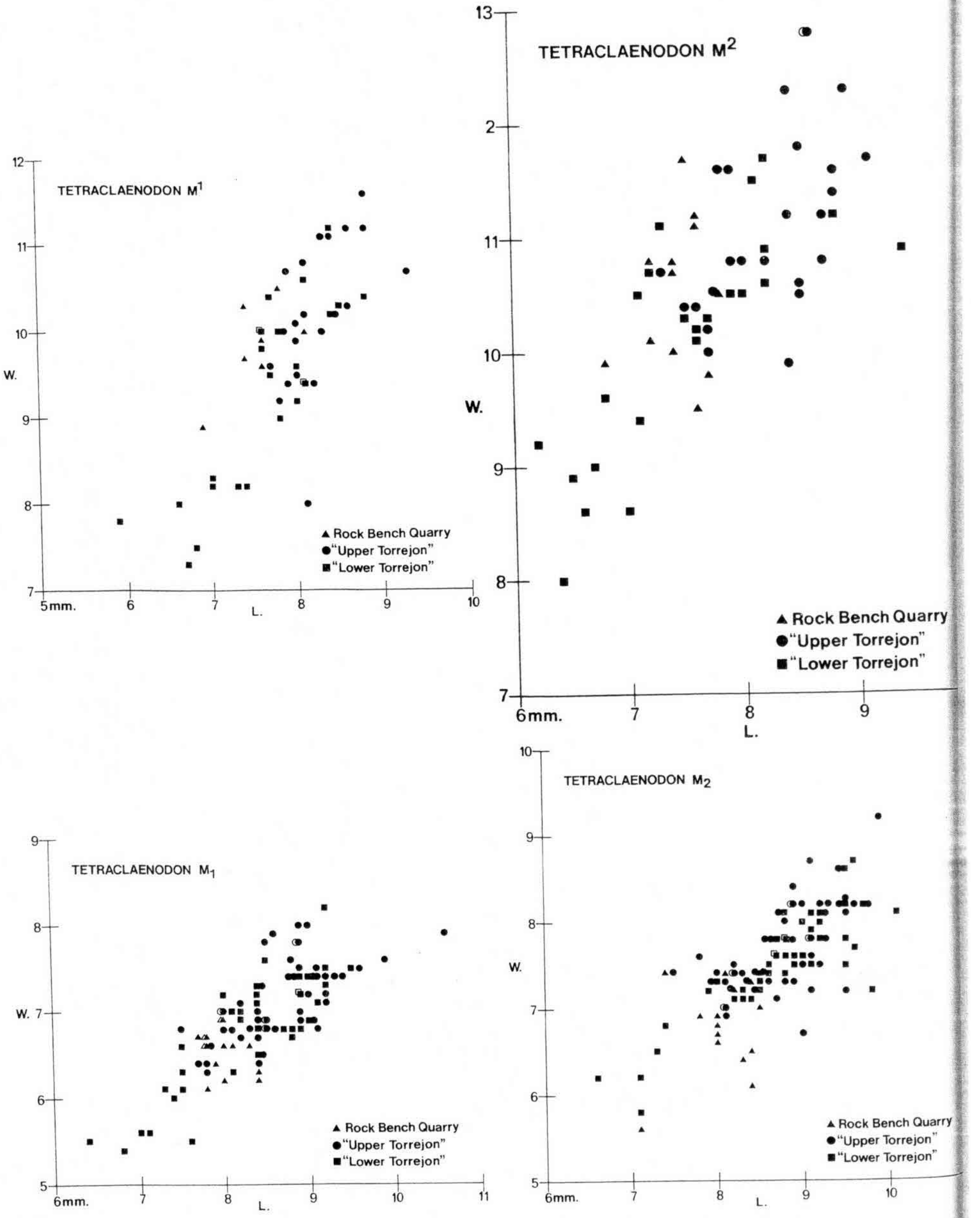


**Figure 5.** Bivariate plots of dimensions of anterior molars of *Tetraclaenodon puercensis.* Localities as in Table 1.

from Rock Bench Quarry in the Ft. Union formation of the northern Bighorn Basin of Wyoming (Jepsen, 1940, pp. 234-236) — and it shows lower coefficients of variation than do the more heterogenous samples from both the lower and the upper parts of the Torrejonian part of the Nacmiento formation of New Mexico. This is to be expected, as the Rock Bench sample is by far the closest to being from a single biologic unit. A more perplexing situation, however, is the considerable difference in variation between the lower Torrejon and upper Torrejon samples. Both were collected from surface localities scattered through over one hundred vertical feet of sediment (Sinclair and Granger, 1914, p. 310-313; Simpson, 1959) and thus undoubtedly represent considerable genetic variation. Nonetheless, the coefficients of variation of the upper Torrejon sample are relatively low. There is no concern that more than a single species, *T. puercensis,* is present there. On the other hand, the sample from the lower Torrejon has no coefficient of variation below 9, and the average size of *Tetraclaenodon* teeth in that sample is slightly smaller than the average size in the upper Torrejon. When these are recalculated with specimens generally attributed to *T. pliciferus* removed, the sizes of the larger animals are almost exactly equal to the upper Torrejon sample and the coefficients of variation much reduced.

If this "improvement" in the statistics were accompanied by a significant morphologic difference, and if the numerical manipulation did not involve assigning teeth from one specimen to two species, there would be evidence for the validity of *T. pliciferus.* In the face of these difficulties, I cannot accept more than a single highly variable species.

*"T. symbolicus"* has been found in later Torrejonian and early Tiffanian rocks in Montana, where *Tetraclaenodon* is much less abundant than it is in New Mexico. It is impossible to distinguish between those specimens and material from the southern localities. In fact, when Simpson established the species (after Gidley's notes), he did so primarily on the basis of geographic separation: "The only constant difference from *T. pliciferus* is greater size, inadequate for specific differentiation were it not correlated with wide geographic separation" (Simpson, 1935b, p. 239). The geographic gaps have since been filled and the size of *"T. symbolicus"* falls rather neatly between the smaller material from New Mexico and the sample from Rock Bench Quarry, and therefore into *T. puercensis.*

The other specimens from assorted localities in Wyoming, Montana, North Dakota and California fit easily into *T. puercensis.* With the exception of the new sample from Swain Quarry (Rigby, in prep., pers. comm.), none are large enough for numerical treatment.

Some poorly defined trends may be followed in *Tetraclaenodon.* Primary among them is the gradual increase in size mentioned

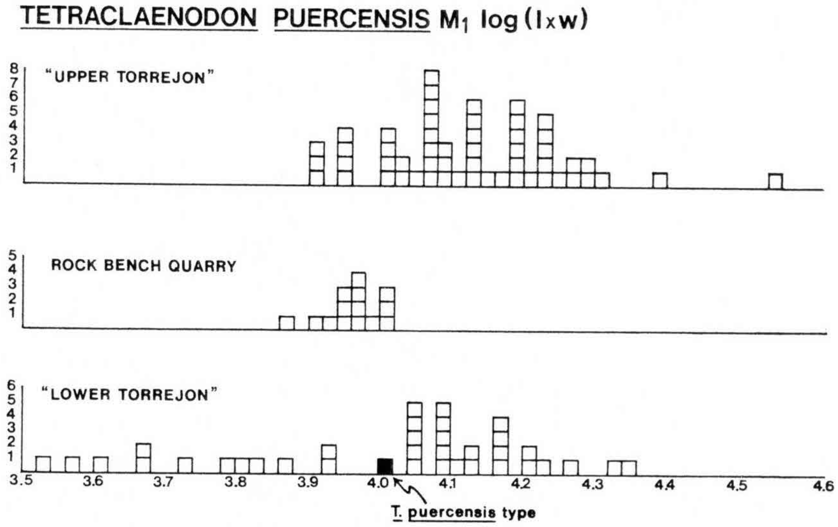


**Figure 6.** Plot of logarithm of the product of length and width measurements of $M_1$ of *Tetraclaenodon puercensis.* Localities as in Table 1.

above and best documented in the New Mexico samples. The Rock Bench Quarry assemblage is closer in size to the lower Torrejon material from New Mexico, but its stratigraphic relationships are not clear. (Rock Bench Quarry is in a channel deposit only about 70 feet above the top of the Puercan Mantua lentil [Jepsen, 1940, p. 234-5], but the amount of downcutting prior to channel filling is uncertain. Sloan [1970] places Rock Bench relatively high in the middle Paleocene.)

If species of *Phenacodus,* with its greater degree of premolar molarization and development of molar styles, may be regarded as progressive, there is some development in that direction through the middle Paleocene. The smaller lower Torrejonian *Tetraclaenodon* specimens have somewhat larger paraconids, more premolariform premolars, and very little development of molar mesostyles. Through the Torrejonian, slight reduction in paraconid development, increase in fourth premolar complexity, and upper molar mesostyle development may be noted.

The relative abundance of *Tetraclaenodon* across its geographic range is instructive. The genus is abundant in New Mexico, common in the central part of its distribution (Swain and Rock Bench quarries), and relatively uncommon in Montana, North Dakota and Alberta, the northern end of its range. This reduction in relative importance from south to north fits with Sloan's (1970) concept of two reasonably distinct North American Paleocene biogeographic provinces with a boundary area in Wyoming. The phenacodonts were an important part of the middle Paleocene southern fauna, but became relatively rare there in later Paleocene and Eocene times.

### *PHENACODUS* Cope, 1873

*Phenacodus* Cope, 1873, Paleo, Bull., No. 17, p. 3.

*Opisthotomus* Cope, 1875, Syst. Cat. Vert. Eoc. New Mex., p. 16.

*Eohyus* Marsh, 1894, Am. Jour. Sci., vol. 48, p. 259.

**Type species**: *P. primaevus* Cope, 1873, Wasatch formation, early Eocene, southwestern Wyoming.

**Included species**: Type species and *P. bisonensis, P. matthewi, P. grangeri, P. brachypternus,* and *P. vortmani* in North America.

**Range**: Late Paleocene to middle Eocene.

**Distribution**: Western North America.

**Diagnosis**: Canines smaller than in *Tetraclaenodon;* postcanine teeth more inflated than in *Tetraclaenodon* or *Ectocion;* premolars more molariform than in *Tetraclaenodon;* $P_3$ with paraconid and metaconid adjacent to dominant protoconid, small low cuspidate talonid; $P_4$ with median paraconid, triangular trigonid, well developed heel with large hypoconid and entoconid small or absent; lower molars bulbous, paraconid weak, though better developed on anterior molars, paralophid always complete; narrow talonid on $M_3$. $P^3$ with both paracone and metacone, slight paraconule development, no hypocone; $P^4$ with enlarged cingulum and occasionally a hypocone, more molariform than in *Tetraclaenodon;* upper molars with prominent mesostyles and parastyles; metaconule on or posterior to line from metacone to hypocone; paraconule on or anterior to line from paracone to protocone; $M_3$ small, with hypocone.

**Discussion**: *Phenacodus* is conservative, varying morphologically very little through its long temporal range. Aside from some *Tetraclaenodon*-like attributes of early Tiffanian species and a few specializations in Eocene species, there is no consequential change. Many of the differences between species of *Phenacodus* seem closely related to size. Systematics of *Phenacodus,* then, becomes a matter of looking for discrete size groupings at any one time, necessitating a statistical approach.

The evolution of *Phenacodus* can be interpreted as a two stage process. In early Tiffanian times three rather primitive species appeared, derivable from *T. puercensis* and differentiated largely by size. They are typified by relatively poor development of molar mesostyles, compact, uninflated molars, and generally non-molariform last premolars; all of these attributes are primitive in the sense that each is more fully developed in later Paleocene and Eocene species of *Phenacodus.* Each species was a relatively minor part of its respective faunal assemblage.

Later in the Tiffanian the second episode of *Phenacodus* evolution produced three abundant, well-known species which dominated in the early Eocene of North America and the genus spread into western Europe (Rich, 1971). In the late Tiffanian and through the early Wasatchian, *Phenacodus* was the dominant medium-sized herbivore in many faunas, especially in Wyoming. In the early Eocene *Phenacodus,* in terms of proportional representation in many faunas and size range, was at its peak, although the genus was uncommon in southern faunas such as Huerfano, San Jose, and Big Bend. This dominance decreased through the later parts of the Wasatchian. Only one specimen is known from definite Bridgerian rocks (West and Atkins, 1970); this is the geologically youngest known occurrence of a representative of the Phenacodontidae.

### *Phenacodus matthewi* Simpson, 1935
(Figures 7, 13; Table 6)

*Phenacodus matthewi* Simpson, 1935a, Am. Mus. Novitates 817, p. 24.

*Phenacodus gidleyi* Simpson, 1935a, Am. Mus. Novitates 817, p. 25.

**Holotype**: AMNH 17191, Mason Pocket, Tiffany formation, early late Paleocene, southern Colorado.

**Range**: Early late Paleocene.

**Distribution**: Southern Colorado.

**Diagnosis**: Small size ($M_1$ approx. 7 mm long); $P_4$ not elongate, with distinct entoconid. Lower molars slightly broader than in *P. brachypternus* and *P. vortmani.* $P^4$ lacking metaconule; upper molars with small mesostyles.

**Discussion**: Simpson (1935a) proposed two species, similar in size, based on two specimens of lower teeth; a third specimen from the same locality in the American Museum collection has since been referred to *P. matthewi.* I agree with Delson (1971, p. 345) that the minor differences used by Simpson are readily accommodated within a normal range of variation and only one small species is represented (Table 6).

Schiebout (1974, pp. 29-30) assigned an additional four specimens from the Tiffanian Black Peaks formation of southwestern Texas to *P. matthewi.* Included in her sample were upper cheek teeth ($P^4$, $M^1$ and $M^2$) referred to *P. matthewi* because of their size relationship to lower teeth more obviously of this species. The illustrations of these teeth show a small mesostyle and a fourth premolar with a paraconule but no metaconule, much like in *P. bisonensis.* The teeth discussed by Schiebout are larger than the *P. matthewi* teeth from Tiffany (Figure 13) but are still smaller than *P. bisonensis.*

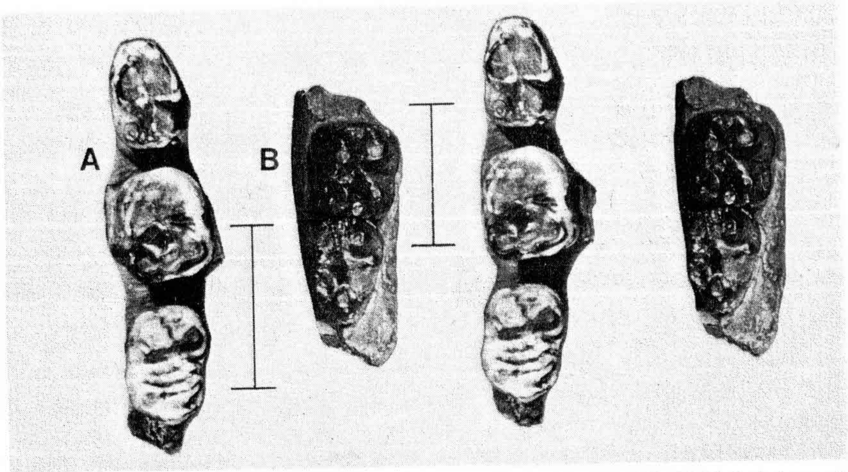


**Figure 7.** *Phenacodus matthewi,* stereophotographs. **A.** AMNH 17193, holotype of *"P. gidleyi",* Tiffany formation, Mason Pocket, Colorado. Right $P_4$, $M_1$, $M_3$. **B.** AMNH 17191, holotype, Tiffany formation, Mason Pocket, Colorado. Right $M_2$-$M_3$. Scale unit represents 1 cm.

### *Phenacodus bisonensis* Gazin, 1956
(Figures 8, 12, 13; Table 7)

*Phenacodus bisonensis* Gazin, 1956a, Smith. Misc. Coll., v. 131, no. 6, p. 44.

**Holotype**: USNM 20564, Saddle Locality, Ft. Union formation, early Tiffanian, Bison Basin, central Wyoming.

**Range**: Early late Paleocene.

**Distribution**: Central Wyoming and central Montana.

**Diagnosis**: Size moderate ($M_1$ length approximately 9 mm); premolars less progressive than in later species, upper molar mesostyles distinct on $M^1$ but weak on $M^2$. $P_4$ paraconid low and far forward; paraconid on $M_1$ well defined, weaker on $M_2$.

**Discussion**: As noted by Gazin (1956a, pp. 45-46), *P. bisonensis* has numerous close similarities to *Tetraclaenodon,* thereby providing good evidence of the course of phenacodont evolution. The degree of premolar molariformity is greater than in any known specimens of *Tetraclaenodon,* and, despite its variability, mesostyle development also is more advanced than in *Tetraclaenodon. P. bisonensis* is distinct morphologically from *T. puercensis,* but also clearly is more primitive than species of *Phenacodus* from the latest Paleocene and early Eocene. It is readily separable on the basis of size from the larger *P. grangeri,* but with some difficulty from the smaller *P. matthewi* (Figure 13).

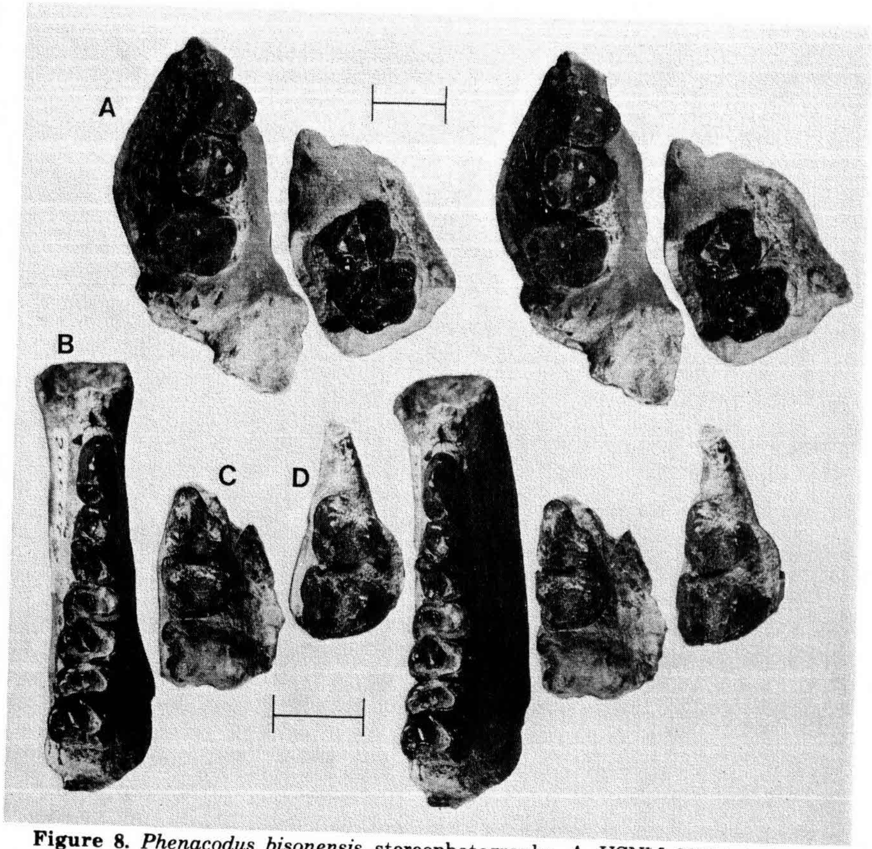


**Figure 8.** *Phenacodus bisonensis,* stereophotographs. **A.** USNM 20564, holotype, Fort Union formation, Bison Basin, Wyoming. Right $P^4$-$M^2$; left $M^1$-$M^2$. **B.** USNM 20567, Fort Union formation, Bison Basin, Wyoming. Right $P^3$-$P^4$. **C.** USNM 20566, Fort Union formation, Bison Basin, Wyoming. Right $P^3$-$P^4$. **D.** USNM 20626, Fort Union formation, Bison Basin, Wyoming. Right $P^3$-$P^4$.
Scale unit represents 1 cm.

*P. bisonensis* is the most abundant species of early Tiffanian phenacodont. It made up approximately 12% of Gazin's original Bison Basin collection (1956a, p. 7) and much additional material from that area has since been collected by Carnegie Museum and the American Museum of Natural History. Unfortunately none of the more recently collected specimens are as complete as these in the original collection, so the anatomy of the species remains essentially unknown.

Several specimens in the Princeton collection, collected in the Tiffanian part of the Crazy Mountain Field, are referable to *P. bisonensis,* thus extending the geographic range north into central Montana.

### *Phenacodus grangeri* Simpson, 1935
(Figures 9-13; Tables 8, 9)

*Phenacodus grangeri* Simpson, 1935a, Am. Mus. Nov. 817, p. 23.

*Tetraclaenodon transitus* Dorr, 1958, Bull. Geol. Soc. Amer., vol. 69, p. 1225.

**Holotype**: AMNH 17185.

**Paratypes**: AMNH 17188, 17187, Mason Pocket, Tiffany formation, early late Paleocene, southern Colorado.

**Range**: Early late Paleocene.

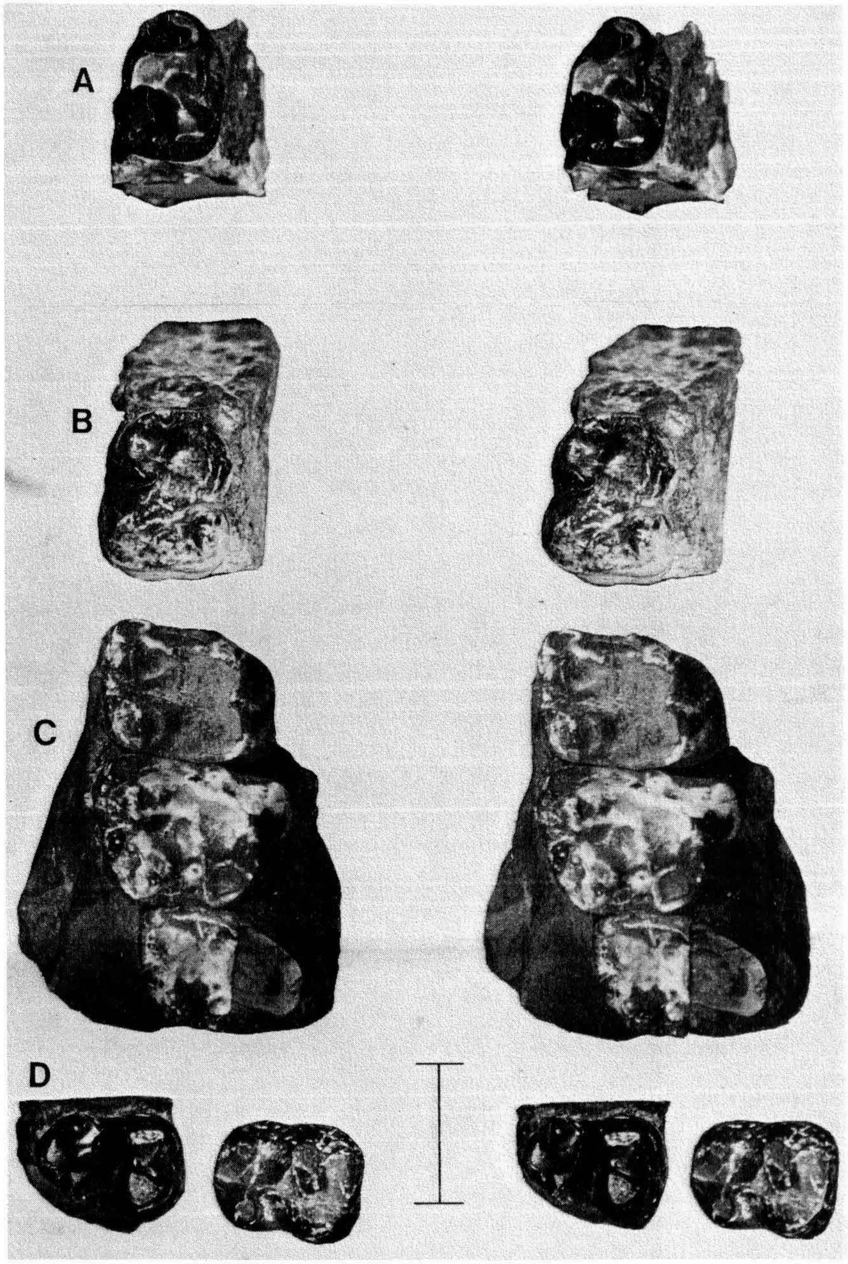
**Distribution**: Colorado and Wyoming.

**Diagnosis**: Size large ($M_1$ length approximately 11 mm); upper molars more transverse than in later species, conules well developed, mesostyle much more prominent on $M^1$ than on $M^2$ and $M^3$, premolars more progressive than *P. bisonensis,* $P_4$ with strong median paraconid; lower molars often with accessory cusps adjacent to metaconid, entoconid or along cristid obliqua.

**Discussion**: The size of *P. grangeri* clearly separates it from the smaller *P. bisonensis* (Figures 12 and 13; Tables 8 and 9). As with the other reasonably well known species of *Phenacodus, P. grangeri* is most abundant toward the northern end of its geographic distribution. The Princeton Cedar Point Quarry in the northern Bighorn Basin has produced a suite of specimens of *P. grangeri;* these confirm Simpson's species determination and add much data on the morphology, as several are almost complete post-canine dentitions while the Tiffany material is isolated teeth and smaller jaw fragments.

Dorr (1958) described a crushed skull from the Paleocene of the Hoback Basin as a new species, *Tetraclaenodon transitus,* in reference to its morphologically intermediate position between *Tetraclaenodon* and *Phenacodus.* Comparison of Dorr's specimen (UMMP 34762) and the other six specimens since referred to *T. transitus* with *P. grangeri* from Cedar Point Quarry suggests that the Hoback material belongs to *Phenacodus* rather than *Tetraclaenodon.* Although there are some morphologic differences from Cedar Point Quarry and Mason Pocket *P. grangeri,* they are of a minor nature, insufficient for specific separation.

Dorr determined that the Battle Mountain locality, the only place from which "*T. transitus*" is known, is late Torrejonian in age. Part of the reasoning for this is the presence of a primitive phenacodont. However, since *Tetraclaenodon* survived into the Tiffanian in Montana, this argument is not a strong one. A more acceptable date for the Battle Mountain fauna is early Tiffanian; the morphologic stage of evolution of *P. grangeri* is compatible with this assignment, which also reflects the ranges of the other elements in the fauna.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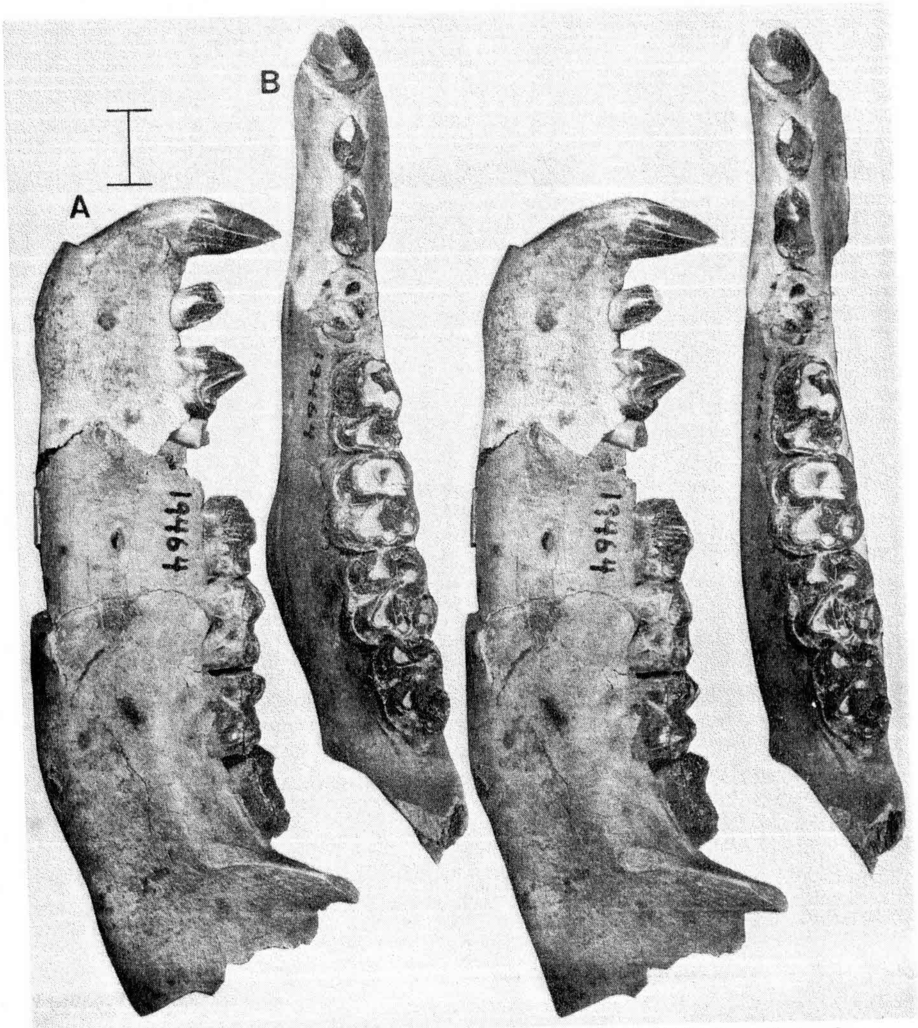


**Figure 10.** *Phenacodus grangeri,* stereophotographs. PU 19464, Fort Union formation, Cedar Point Quarry, Wyoming. Left $P^3$-$M^3$. **A.** Labial view. **B.** Occlusal view.

← **Figure 9.** *Phenacodus grangeri,* stereophotographs. A. AMNH 17177, paratype Tiffany formation, Mason Pocket, Colorado. Right $P_4$. B. AMNH 17188, paratype Tiffany formation, Mason Pocket, Colorado. Left $M_1$. C. AMNH 17185, holotype, Tiffany formation, Mason Pocket, Colorado. Right $M^1$-$M^3$. D. AMNH 17198, paratype Tiffany formation, Mason Pocket, Colorado. Right $M_2$, $M_3$.

Scale unit represents 1 cm.

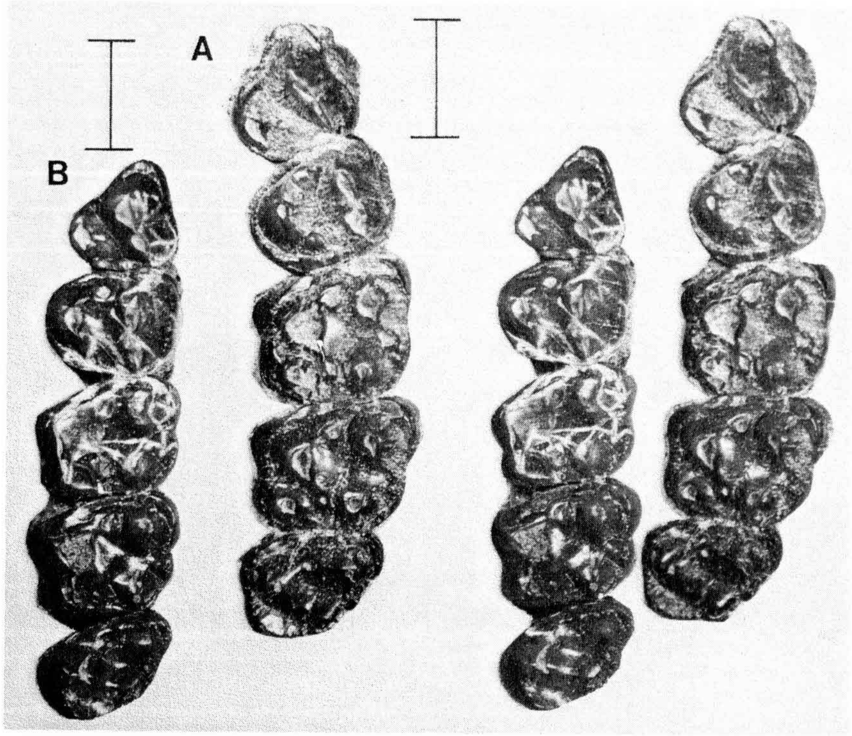


**Figure 11.** *Phenacodus grangeri,* stereophotographs. **A.** PU 19582, Fort Union formation, Cedar Point Quarry, Wyoming. Left $P^3$-$M^3$. **B.** PU 19924, Fort Union formation, Cedar Point Quarry, Wyoming. Left $P^3$-$M^3$.
Scale unit represents 1 cm.

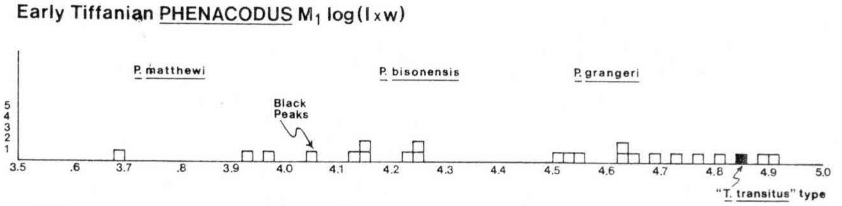


**Figure 12.** Plot of logarithm of the product of length and width measurements of $M_1$ of early Tiffanian species of *Phenacodus.*

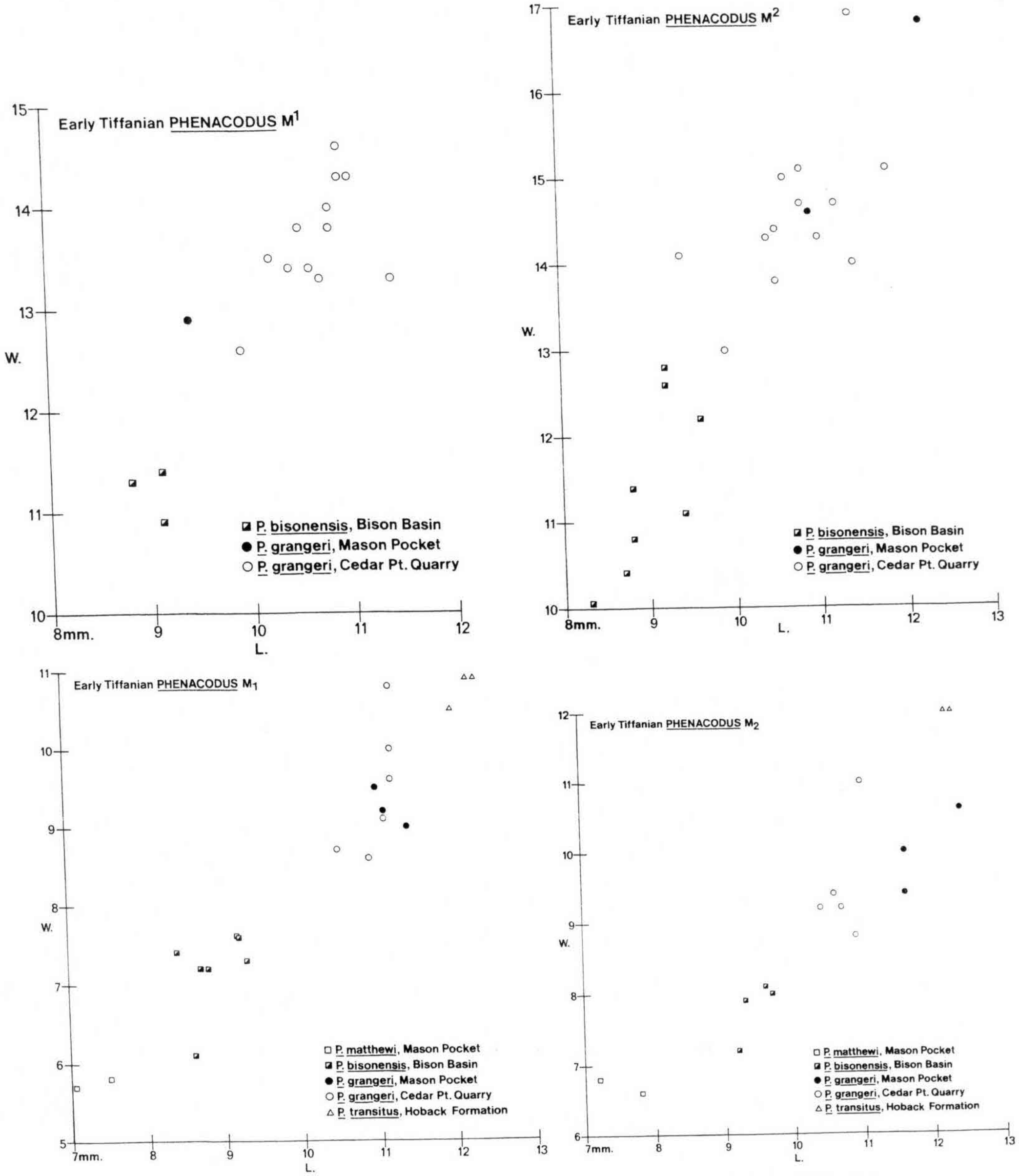


**Figure 13.** Bivariate plots of dimensions of anterior molars of early Tiffanian species of *Phenacodus*. Localities as in Table 1.

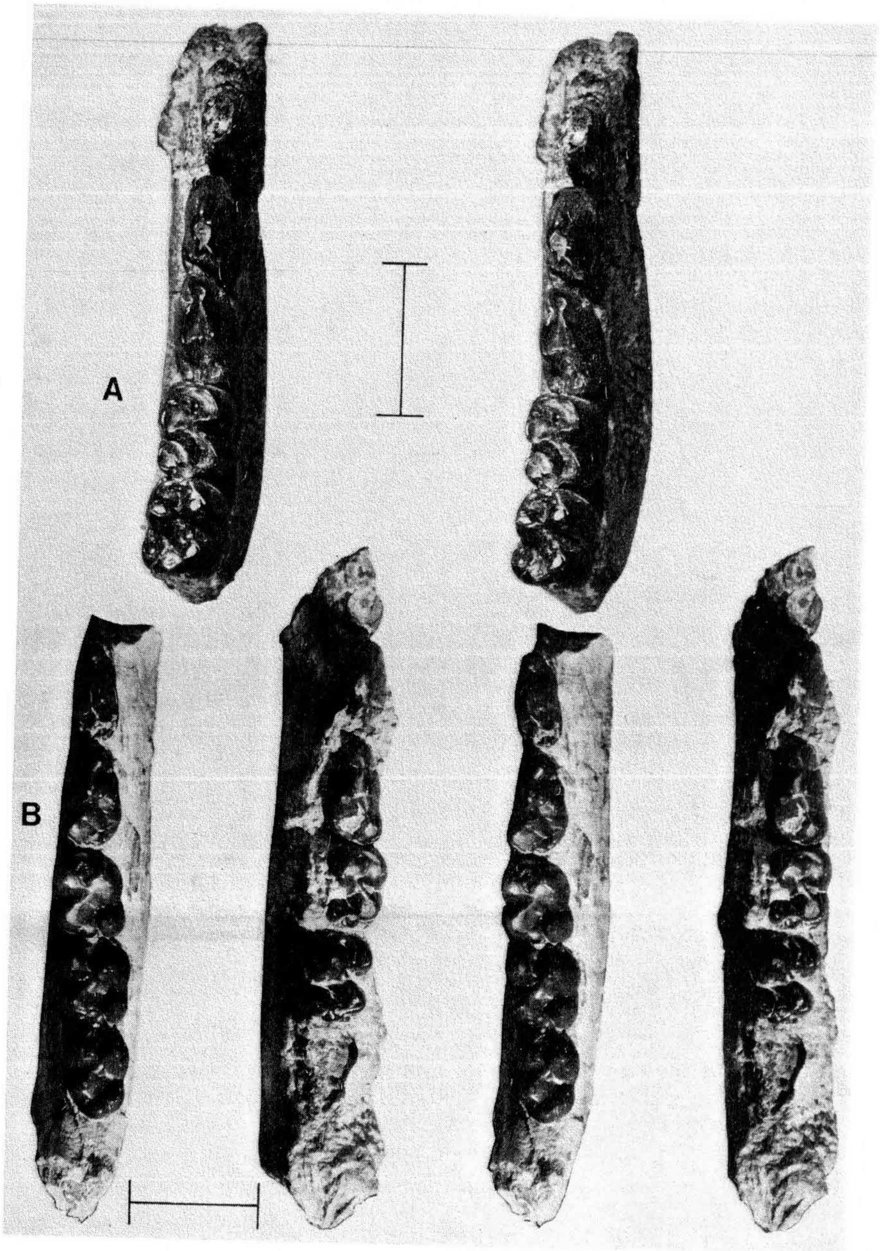


**Figure 14.** *Phenacodus brachypternus*, stereophotographs. **A.** PU 20214, Willwood formation, Graybull beds, Bighorn Basin, Wyoming. Right $P_3$-$M_2$. **B.** AC 3544, Willwood formation, Graybull beds, Bighorn Basin, Wyoming. Right $P_3$-$M_2$; left $P_3$-$M_3$. Scale unit represents 1 cm.

### *Phenacodus brachypternus* Cope, 1882
(Figures 14, 15, 24-26; Table 10)

*Phenacodus brachypternus* Cope, 1882c, Proc. Am. Phil. Soc., vol. 20, p. 180.

**Holotype**: AMNH 4396, Graybull beds, Willwood formation, early Eocene, Bighorn Basin, Wyoming.

**Range**: Early Eocene.

**Distribution**: Wyoming, Colorado and New Mexico.

**Diagnosis**: Size small ($M_1$ length less than 7 mm); premolars narrow and elongate; $P_3$ with low heel; $P_4$ with prominent paraconid; molars typical of genus, but metaconules weak.

**Discussion**: The small size and elongate premolars immediately distinguish *P. brachypternus* from all other species (Figures 24-26). McKenna (1960, p. 101) regarded *P. brachypternus* as highly distinct and its assignment to *Phenacodus* as possibly questionable. I do not believe that the specific attributes of *P. brachypternus* are so

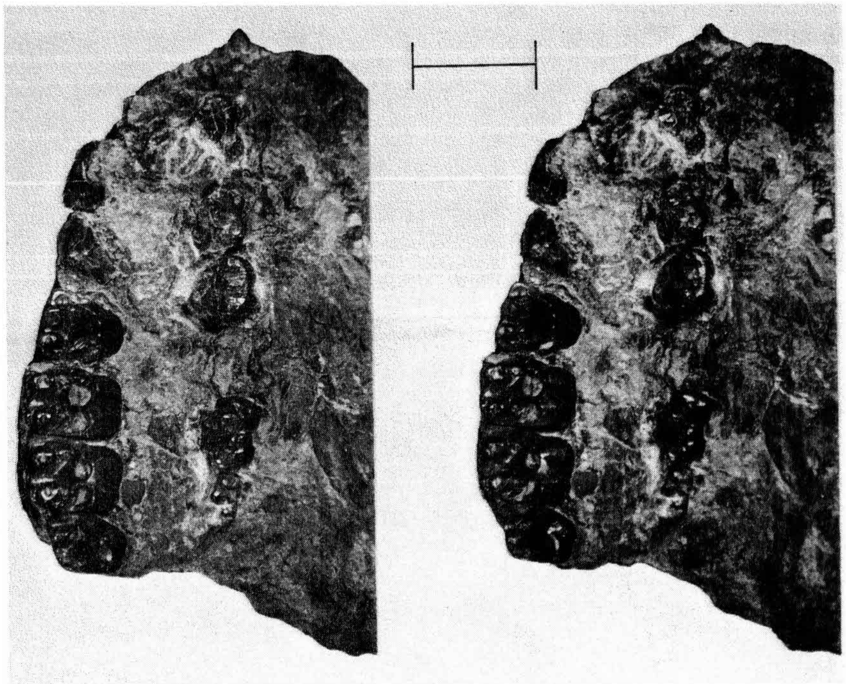


**Figure 15.** *Phenacodus brachypternus,* stereophotographs. AMNH 15766, Willwood formation, Graybull beds, Bighorn Basin, Wyoming. Right $P^2$-$M^3$. Scale unit represents 1 cm.

marked as to remove it from *Phenacodus;* rather it is simply small (Table 10), gracile and has a somewhat elongate premolar dentition.

The temporal range of *P. brachypternus* is rather interesting as it appears in some numbers in the early Wasatchian. No predecessors have yet been found in the latest Paleocene, and only a single specimen (AMNH 12788) has been found in strata postdating the Graybull. *P. brachypternus* does not seem to have left any descendants.

### *Phenacodus vortmani* Cope, 1880
(Figures 16-18, 23-28; Tables 11-16)

*Hyracotherium vortmani* Cope, 1880, Amer. Nat., v. 14, p. 747.

*Phenacodus apternus* Cope, 1882c, Proc. Am. Phil. Soc., vol. 20, p. 180.

*Phenacodus copei* Granger, 1915, Bull. Am. Mus. Nat. Hist., vol. 34, p. 344.

*Ectocion collinus* Russell, 1929, Am. J. Sci., v. 17, p. 177.

*Phenacodus almiensis* Gazin, 1956b, Smiths, Misc. Coll., vol. 131, no. 7, p. 13.

**Holotype**: AMNH 4824, Lost Cabin beds, Wind River formation, late early Eocene, Wind River Basin, Wyoming.

**Range**: Latest Paleocene and early Eocene.

**Distribution**: New Mexico, Colorado and Wyoming.

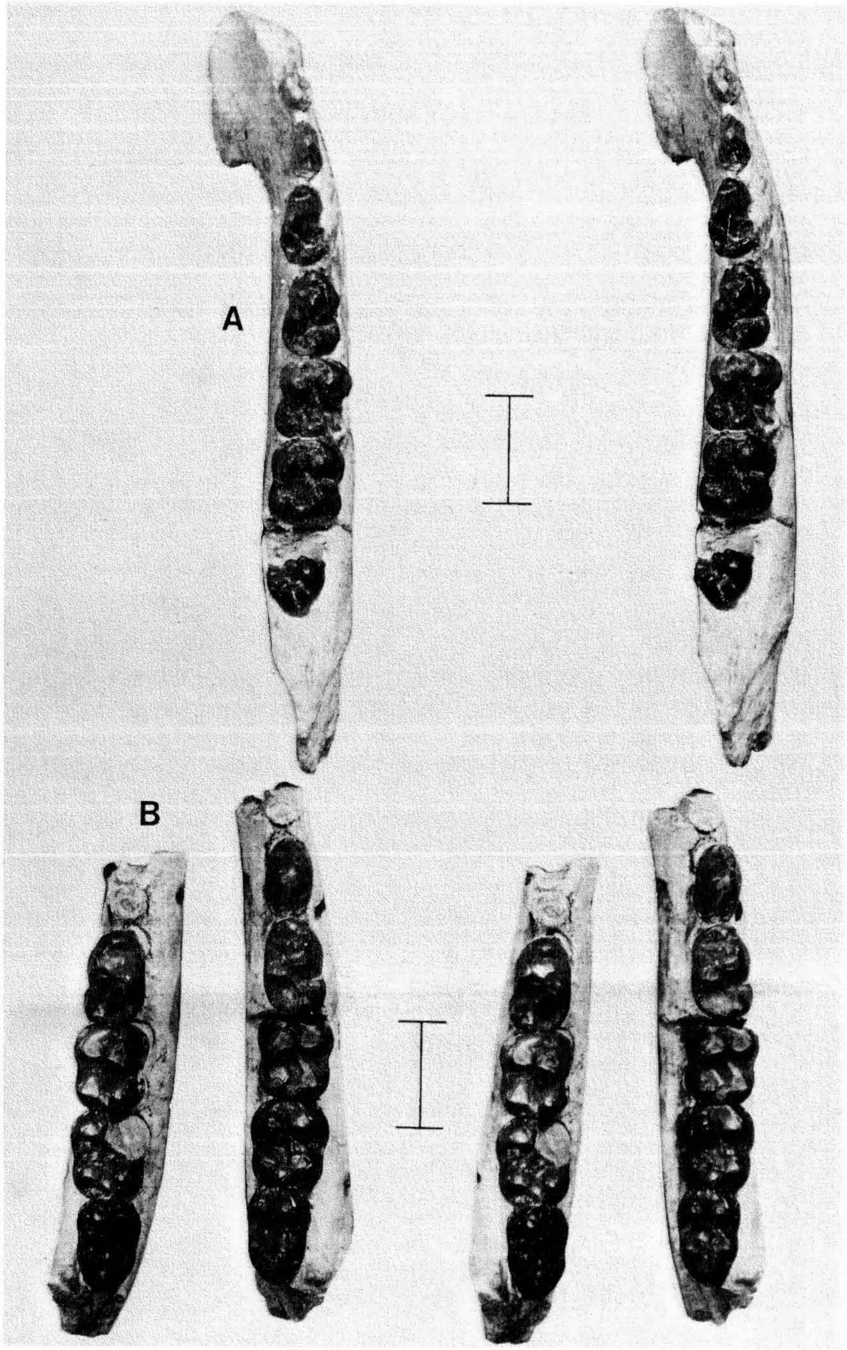
**Diagnosis**: Size moderate ($M_1$ length 7.5 to 10 mm); premolars more compact and progressive than *P. brachypternus;* upper premolar and molar parastyles large; molars typical of genus.

**Discussion**: A prominent moderate-sized group, well separate from *P. brachypternus* and less distinctly separate from the larger *P. primaevus,* shows up in bivariate plots (Figures 23-26, 28) of late Tiffanian and Wasatchian *Phenacodus.* Coefficients of variation on this group are well within the limits of a single species (Tables 11-16), and there is no evidence of more than the single cluster of points. Granger (1915, p. 344) proposed separation of a group of somewhat larger specimens in the Graybull sample as a distinct species, *P. copei.* The differences he cited, however, are simply intraspecific variation (Guthrie, 1967, pp. 40-41).

Gazin (1956b, p. 13) proposed *P. almiensis* for a sample of moderate-sized *Phenocodus* from the late Tiffanian Buckman Hollow locality in western Wyoming. These specimens average about 10% larger than *P. vortmani* from the northern Wyoming early Wa-

**Figure 16.** *Phenacodus vortmani,* stereophotographs. **A.** AMNH 14787, Wind River formation, Lost Cabin beds, Wind River Basin, Wyoming. Right $P_1$-$M_3$. **B.** AMNH 4380, Willwood formation, Graybull beds, Bighorn Basin, Wyoming. Left $P_4$-$M_3$; right $P_3$-$M_3$.

Scale unit represents 1 cm. →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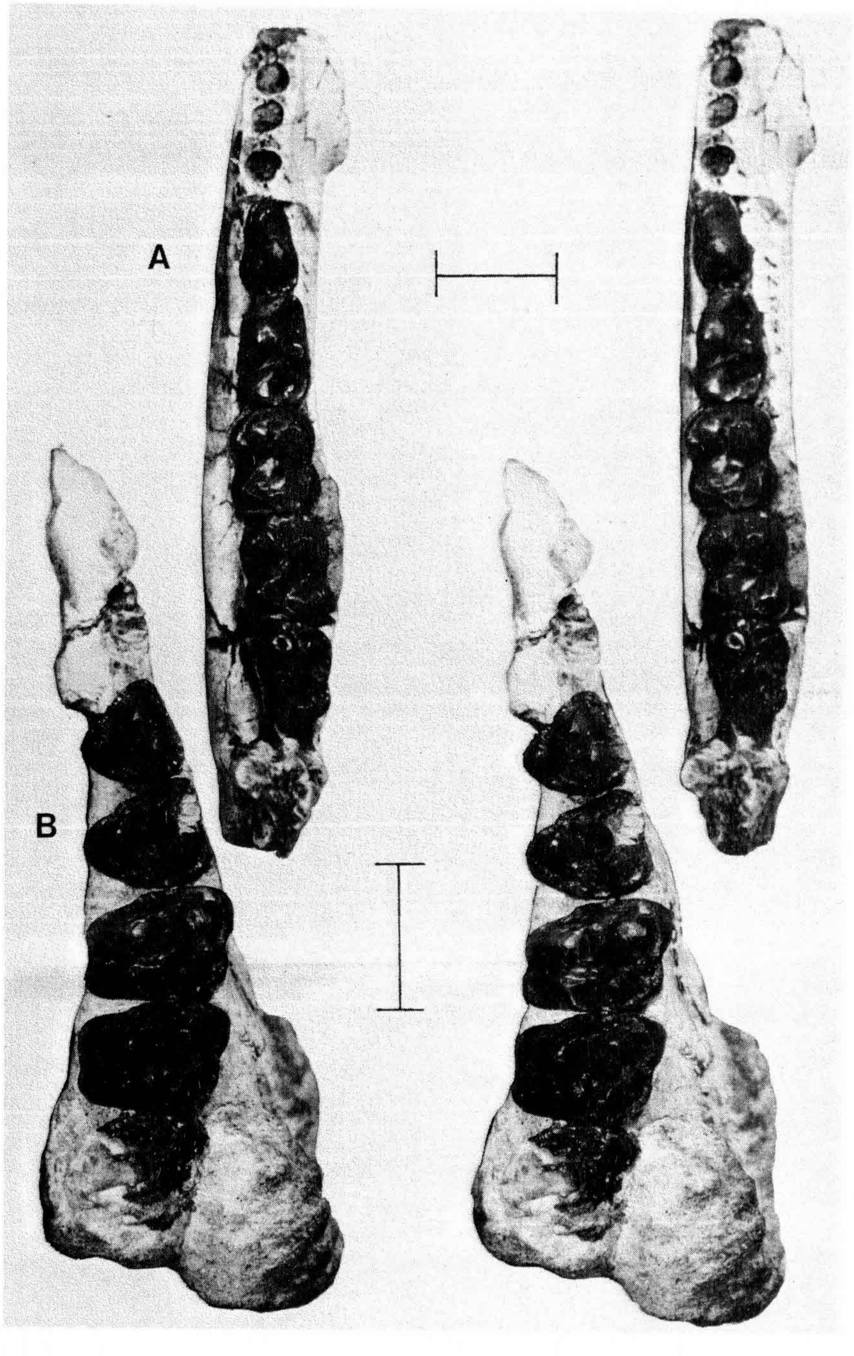
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satchian and are just about the same size as materials from the late Tiffanian Polecat Bench area of northern Wyoming. Aside from the somewhat larger size, Gazin suggested that the premolars of the Buckman Hollow specimens were more advanced than in *P. vortmani.* While this is true for the holotype of *P. almiensis* (USNM 16691), most of the other specimens show $P^4$s without hypocones and with small conules, typical of other late Tiffanian *Phenacodus.* I regard these features as minor variations of a local population of *P. vortmani.*

The greater size of the Buckman Hollow and Polecat Bench assemblages accentuates the general decrease in size in the *P. vortmani* lineage noted by Guthrie (1967, pp. 41). Tables 11-16 demonstrate this trend.

*Ectocion collinus* (Russell, 1929) is based on a single isolated $M^3$ which has a prominent hypocone. A hypocone is characteristic of *Phenacodus* rather than *Ectocion* and the pattern of cusp organization is indicative of *Phenacodus*. The dimensions of the tooth fall well within the known range for *P. vortmani.* I believe it is reasonable to incorporate *E. collinus* into *P. vortmani* and extend the species range north into Alberta.

*Phenacodus vortmani* is well known morphologically, as a virtually complete skeleton has been found. This (AMNH 4378) was described by Cope (1884, pp. 464-487).

By the later part of the Wasatchian (Lysite and Lost Cabin time), *P. vortmani* was the dominant phenacodont in collections from Wyoming, as *P. brachypternus* was essentially extinct and *P. primaevus* much reduced in numbers.

### *Phenacodus primaevus* Cope, 1873
(Figures 19-28; Tables 17-18)

*Phenacodus primaevus* Cope, 1873, Palaeont. Bull., no. 17, p. 3.

*Phenacodus omnivorus* Cope, 1874, Rept. Fos. Vert. N. Mex., p. 11.

*Phenacodus trilobatus* Cope, 1881c, Bull. U.S. Geog. & Geog. Surv. Terr., v. 6, p. 200.

*Phenacodus nunienus* (in part) Cope, 1884, Tert. Vert., p. 434.

*Phenacodus hemiconus* Cope, 1882c, Proc. Am. Phil. Soc., v. 20, p. 179.

*Phenacodus intermedius* Granger, 1915, Bull. Am. Mus. Nat. Hist., v 34, p. 340.

← **Figure 17.** *Phenacodus vortmani,* stereophotographs. **A.** AMNH 16871, Wind River formation, Lysite beds, Wind River Basin, Wyoming. Left $P_3$-$M_3$. **B.** AMNH 2983, Wind River formation, Lost Cabin beds, Wind River Basin, Wyoming. Left $P^3$-$M^2$. Scale unit represents 1 cm.

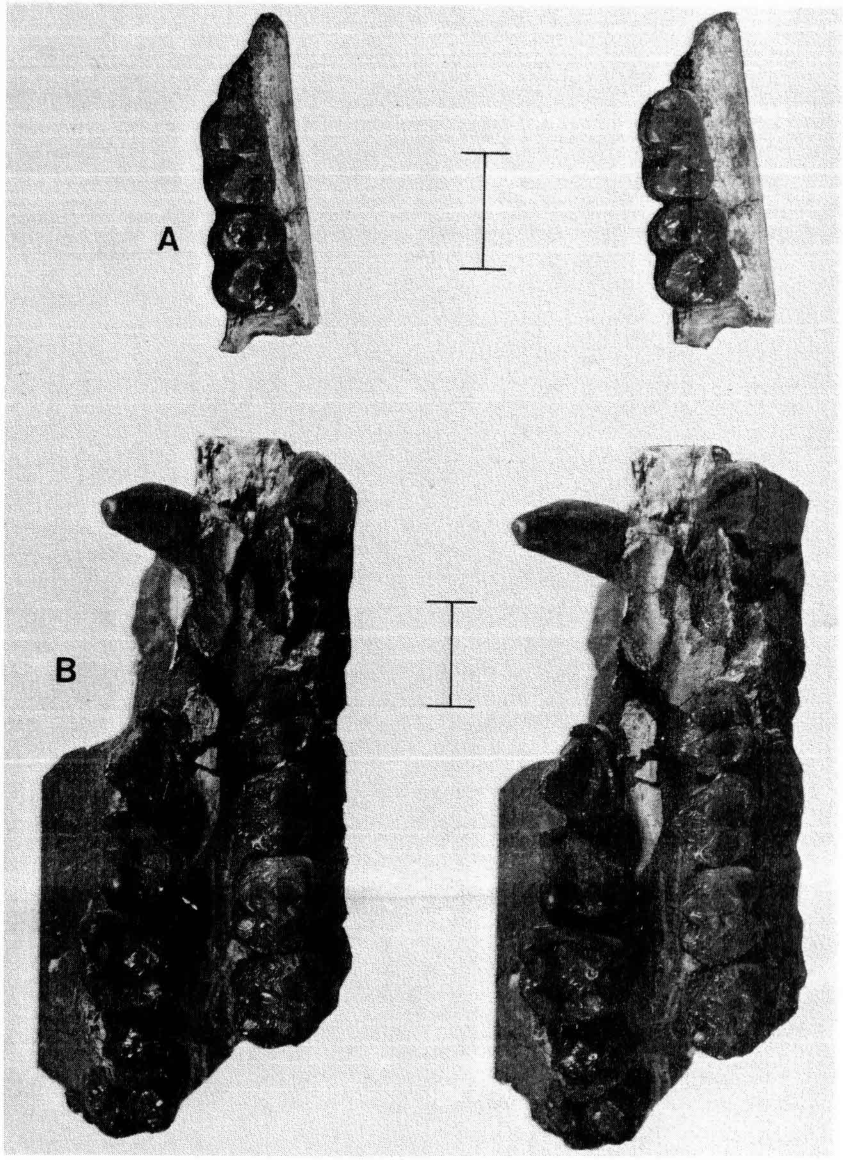


**Figure 18.** *Phenacodus vortmani,* stereophotographs. **A.** USNM 20643, Almy formation, Buckman Hollow, Wyoming. Left $P_4$-$M_1$. **B.** USNM 16691, holotype of "*P. almiensis*", Almy formation, Buckman Hollow, Wyoming. Right C, $P^3$-$M^2$; left C, $P^3$-$M^3$.

Scale unit represents 1 cm.

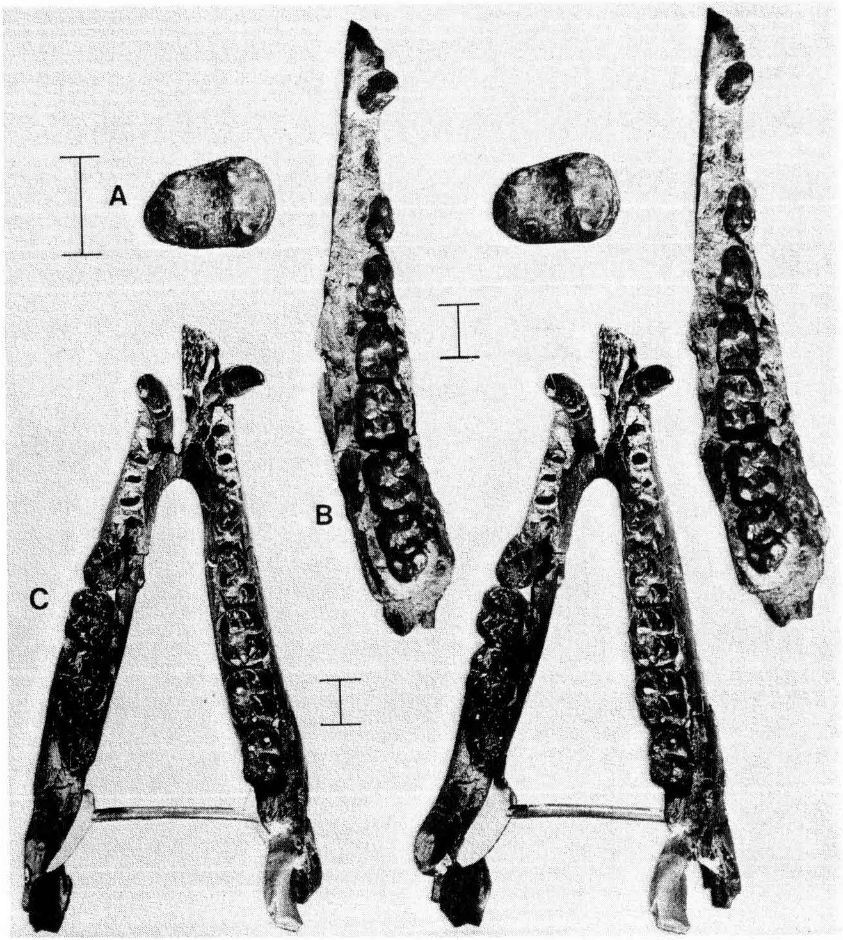


**Figure 19.** *Phenacodus primaevus,* stereophotographs. **A.** AMNH 4408, holotype, Wasatch formation, Evanston, Wyoming. Left $M_3$. **B.** PU 13147, Fort Union formation, upper Polecat Bench beds, Bighorn Basin, Wyoming. Right C, $P_2$-$M_3$. **C.** PU 18742, Willwood formation, Graybull beds, Bighorn Basin Wyoming. Right C, $P_3$-$M_3$; left C, $P_4$-$M_3$.

Scale unit represents 1 cm.

*Phenacodus robustus* (Granger, 1915) Simpson, 1937, Am. Mus. Novitates 954, p. 17.

**Holotype**: AMNH 4408, Wasatch formation, early Eocene, Bear River, Wyoming.

**Plesiotype**: AMNH 4369, Graybull beds, Willwood formation, early Eocene, Bighorn Basin, Wyoming.

**Range**: Latest Paleocene to middle Eocene.

**Distribution**: Western North America.

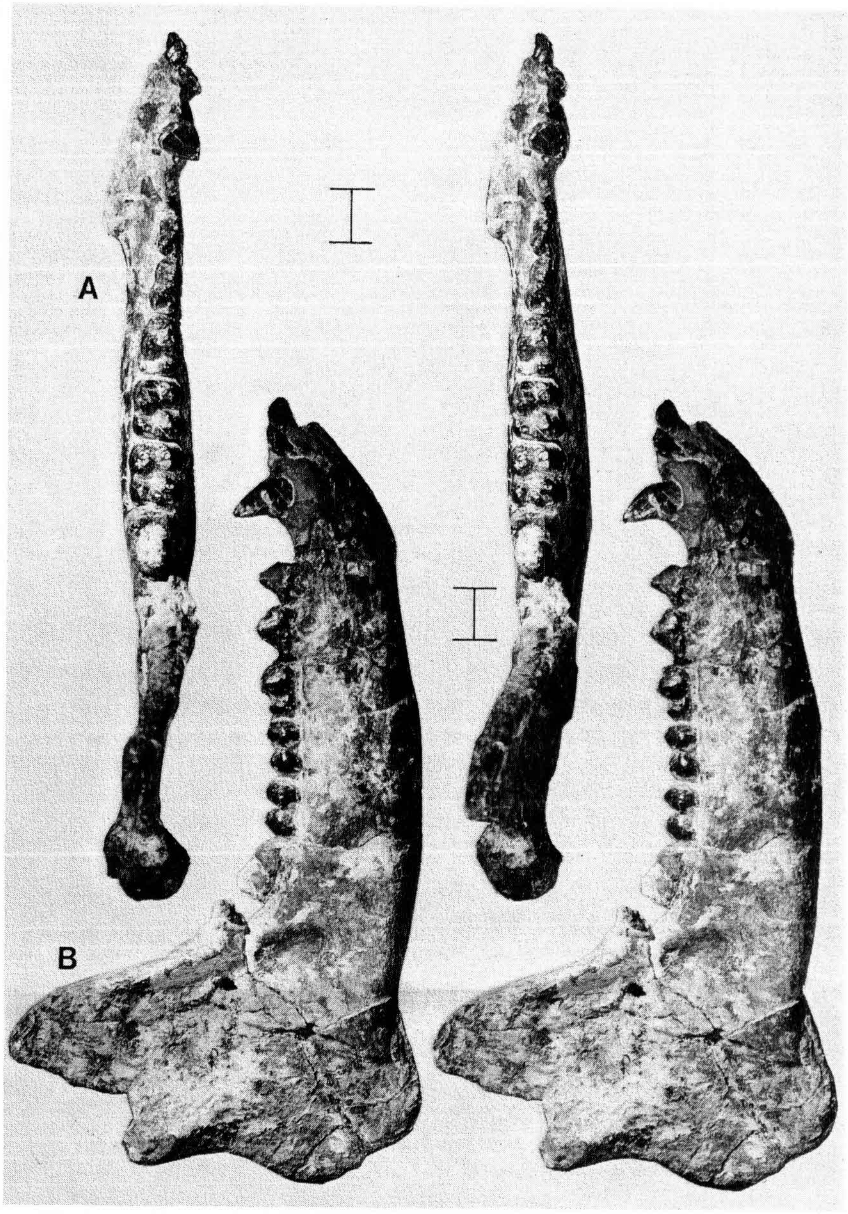


**Figure 20.** *Phenacodus primaevus,* stereophotographs. CM 15350, Willwood formation, Graybull beds, Bighorn Basin, Wyoming. Right $I_2$-$M_3$. **A.** Occlusal view. **B.** Labial view.

Scale unit represents 1 cm.

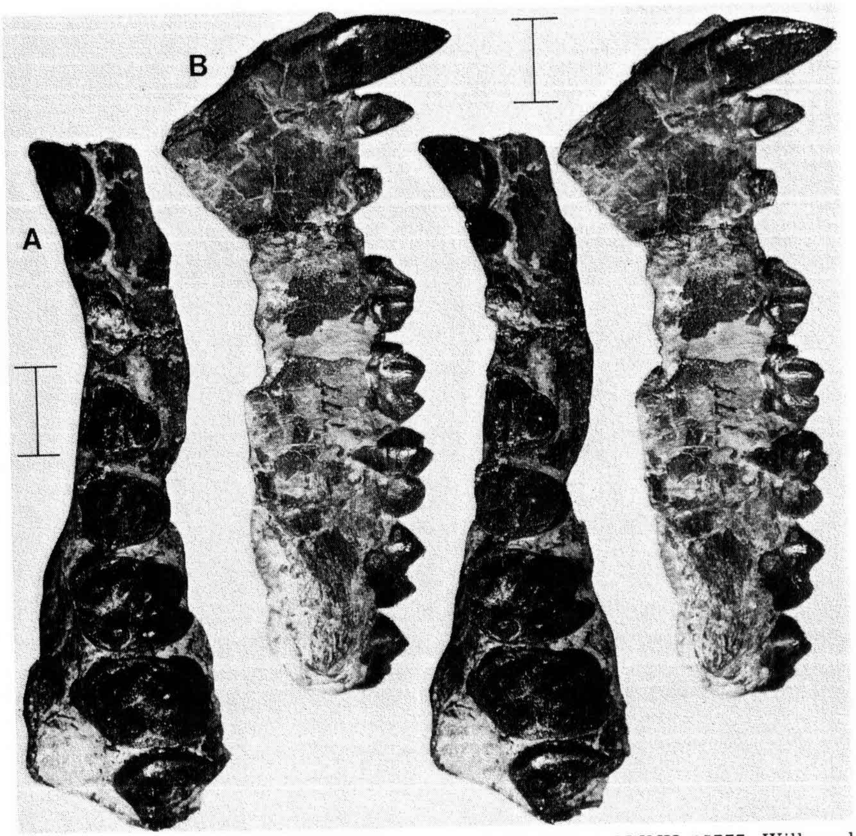


**Figure 21.** *Phenacodus primaevus,* stereophotographs. AMNH 15777, Willwood formation, Graybull beds, Bighorn Basin, Wyoming. Right C-$M^3$. **A.** Occlusal view. **B.** Labial view.

Scale unit represents 1 cm.

**Diagnosis**: Size large ($M_1$ length exceeds 10 mm); fourth premolars markedly molariform; molars bulbous and inflated, mesostyles well developed.

**Discussion**: This is the best known, most abundant and longest ranging species of *Phenacodus.* Several skulls and skeletons are available for study; the two finest specimens are in the collections of the American Museum of Natural History (AMNH 4369) and Princeton University (PU 14864). AMNH 4369 has been described and illustrated by Cope (1884, pp. 435-463) and by Osborn (1898); the Princeton specimen, which is more complete, remains undescribed.

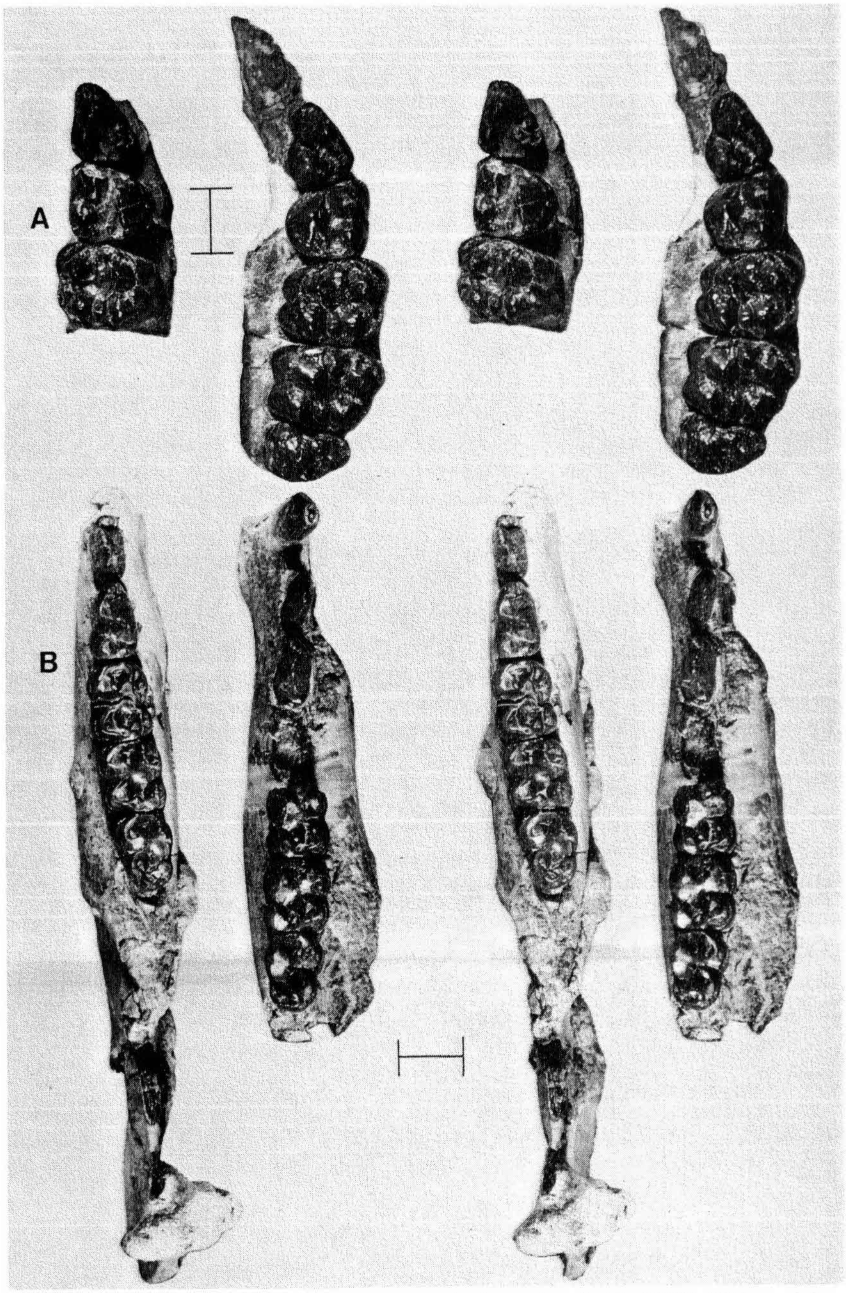


**Figure 22.** *Phenacodus primaevus,* stereophotographs. **A.** PU 16198, Willwood formation, Graybull beds, Bighorn Basin, Wyoming. Right $P^4$-$M^1$; left $P^4$-$M^3$. **B.** PU 13227, Willwood formation, Graybull beds, Bighorn Basin, Wyoming. Right and left C, $P^3$-$M^3$. Scale unit represents 1 cm.

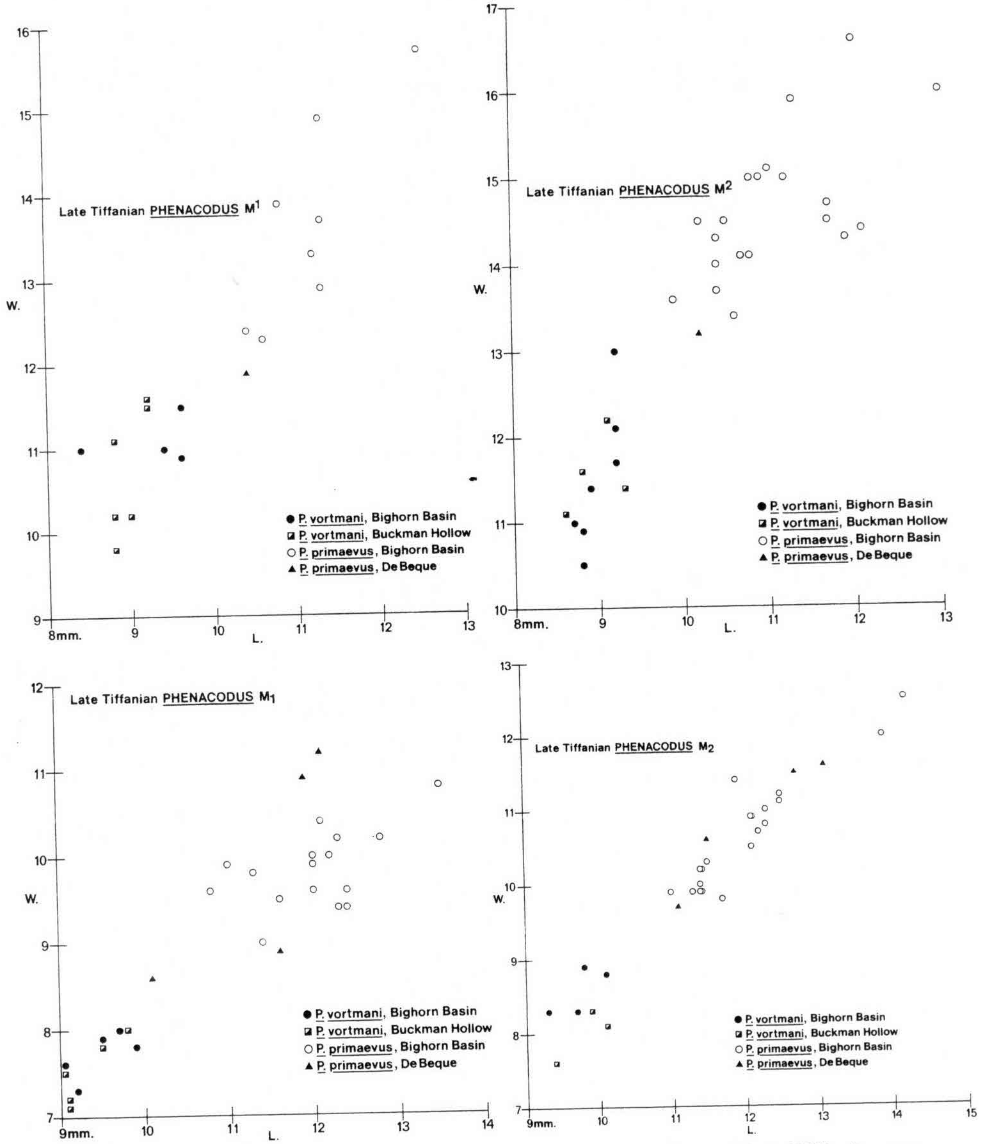


**Figure 23.** **Bivariate plots of dimensions of anterior molars of late Tiffanian species of** *Phenacodus*. Localities as in Table 1.

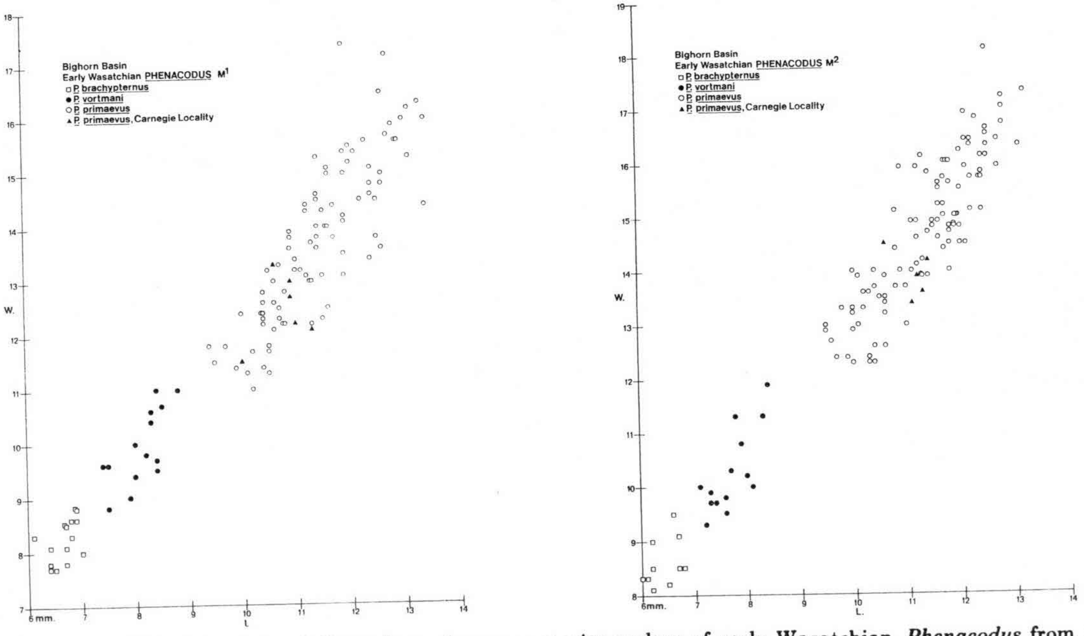


**Figure 24.** Bivariate plots of dimensions of upper anterior molars of early Wasatchian *Phenacodus* from the Bighorn Basin.

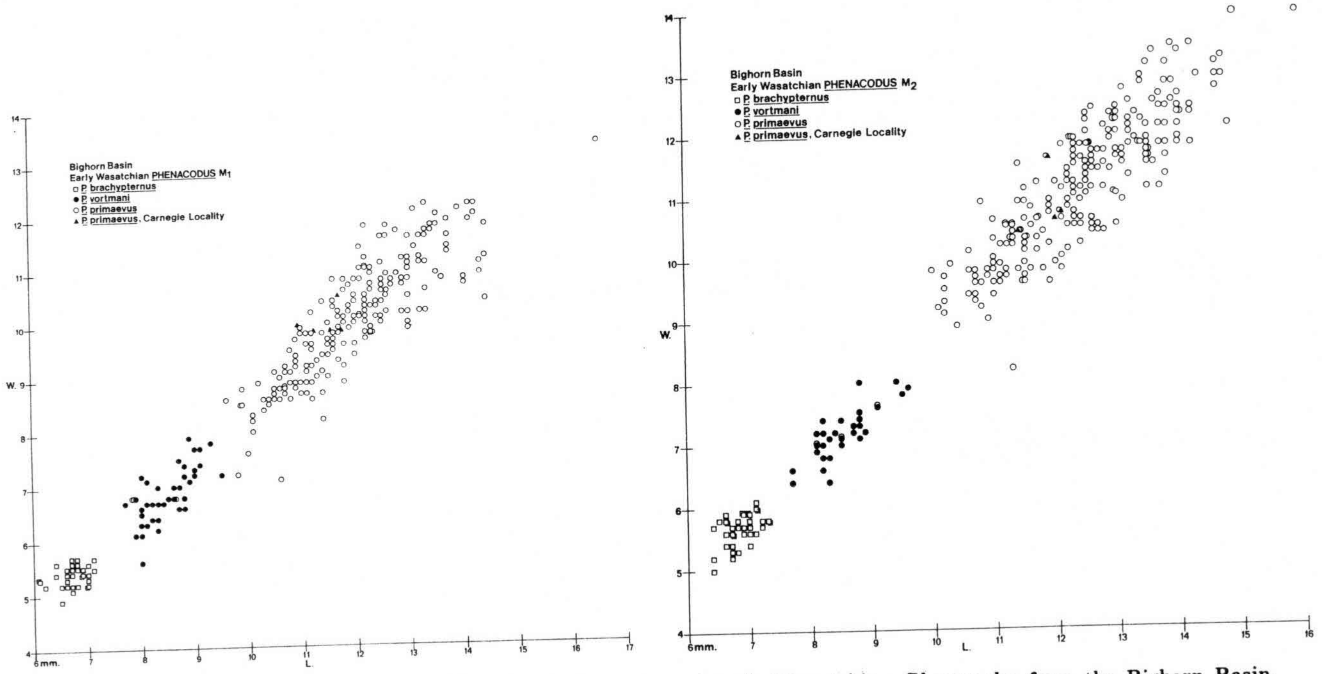


**Figure 25.** Bivariate plots of dimensions of lower anterior molars of early Wasatchian *Phenacodus* from the Bighorn Basin.

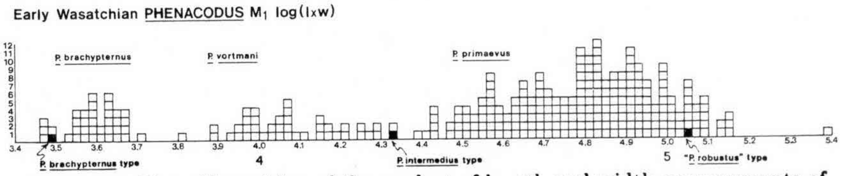


**Figure 26.** Plot of logarithm of the product of length and width measurements of $M_1$ of early Wasatchian species of *Phenacodus*.

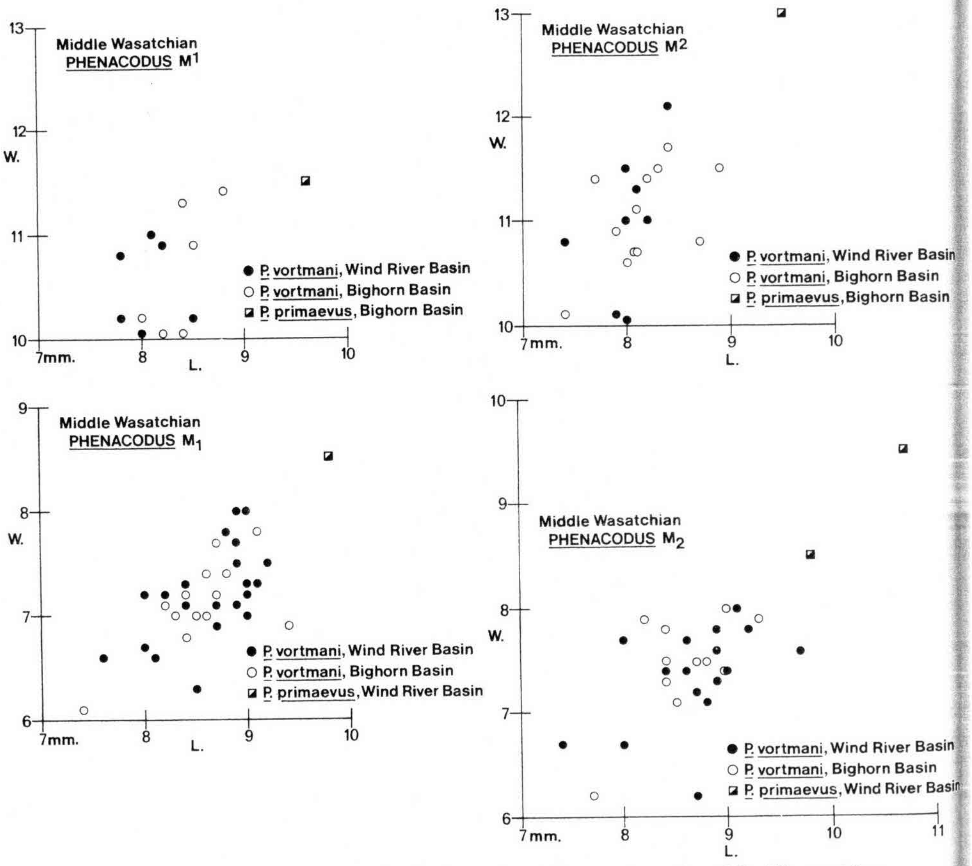


**Figure 27.** Bivariate plots of dimensions of anterior molars of middle Wasatchian species of *Phenacodus*. Localities as in Table 1.

Various attempts have been made to subdivide Eocene *P. primaevus* into two or more species (Granger, 1915; Simpson, 1937b; Guthrie, 1971). The most common approach has been to designate the slightly smaller specimens *P. intermedius* and the larger ones *P. robustus*. The present consideration of large samples has produced coefficients of variation (Tables 17 and 18) which are high but very close to the single-species range indicated by Gingerich (1974). Those specimens in various collections designated as *P. intermedius*

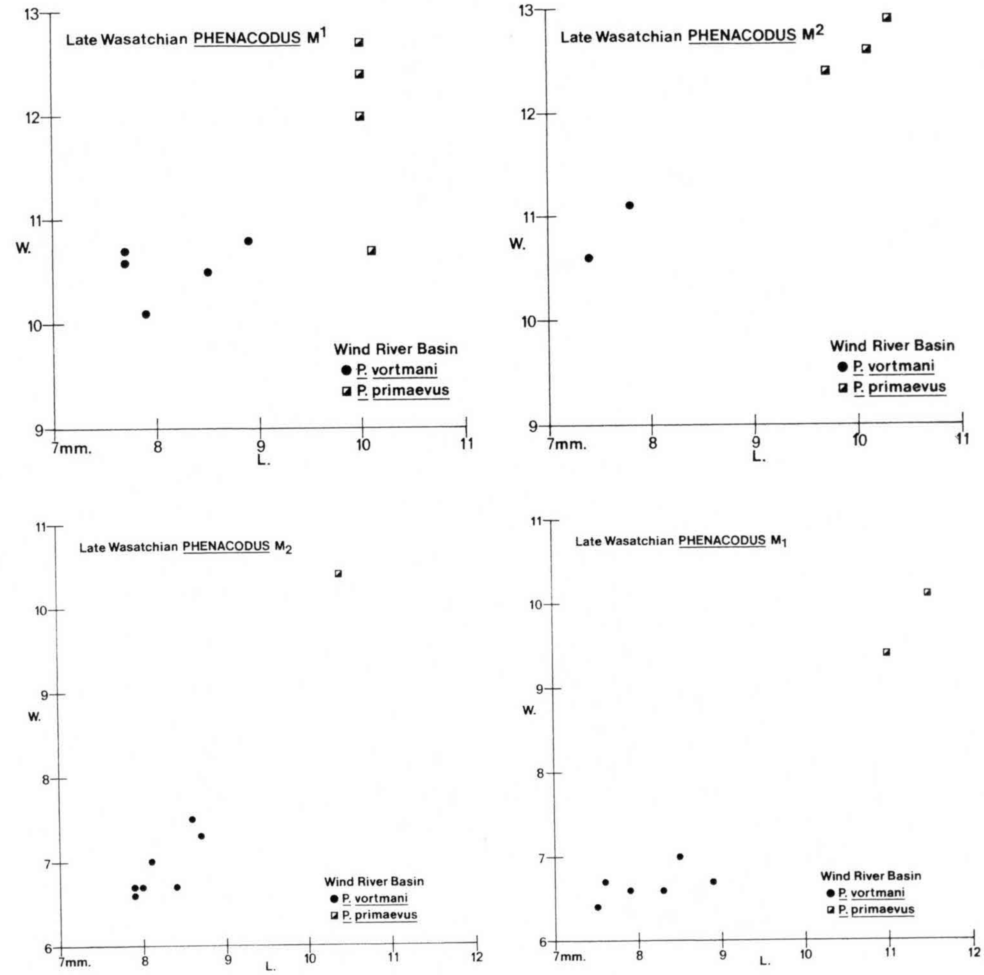


**Figure 28.** Bivariate plots of dimensions of anterior molars of late Wasatchian *Phenacodus* from the Wind River Basin.

and *P. robustus* grade almost imperceptibly into the mass of material generally agreed upon as *P. primaevus*. There are no consequential morphologic differences between the larger and smaller specimens in this suite.

Despite the long temporal range the size of *P. primaevus* remained constant (Tables 17 and 18). The only change is a slight increase in inflation of the postcanine teeth in the later specimens.

The species is most abundant in northern Wyoming, with the largest collection coming from late Tiffanian and early Wasatchian rocks of the Bighorn Basin.

### *PROSTHECION* Patterson and West, 1973

*Prosthecion* Patterson and West, 1973, Breviora no. 403, p. 2.

**Type species**: *Prosthecion major* Patterson and West, 1973, DeBeque formation, late Paleocene, Western Colorado.

**Included species**: Type species only.

**Range**: Late Paleocene.

**Distribution**: Western Colorado.

**Diagnosis**: Moderate-sized phenacodont; approximately the same size as *Phenacodus bisonensis* and *P. vortmani*, larger than *Ectocion wyomingensis* and *E. osbornianum*. Upper premolars with complete cingulum and smaller conules and parastyle than in *Ectocion*. $P^3$ shorter and wider than in *Ectocion*, with separate metacone and paracone. Upper molars similar to those of *Ectocion*. $P_3$ with strong paraconid, distinct metaconid, rudimentary protostylid, and hypoconid surrounded posteriorly by a cingulum; heel broader than in *Ectocion*. $P_4$ with hypoconid more central in position than in later *Ectocion*, entoconid not differentiated, rudiments of protostylid and metastylid present. Lower molars intermediate between those of *Ectocion* and *Phenacodus*, moderately robust and lacking well-developed paraconid, especially in posterior premolars.

### *Prosthecion major* Patterson and West, 1973
(Figure 29)

*Prosthecion major* Patterson and West, 1973, Breviora no. 403, p. 2.

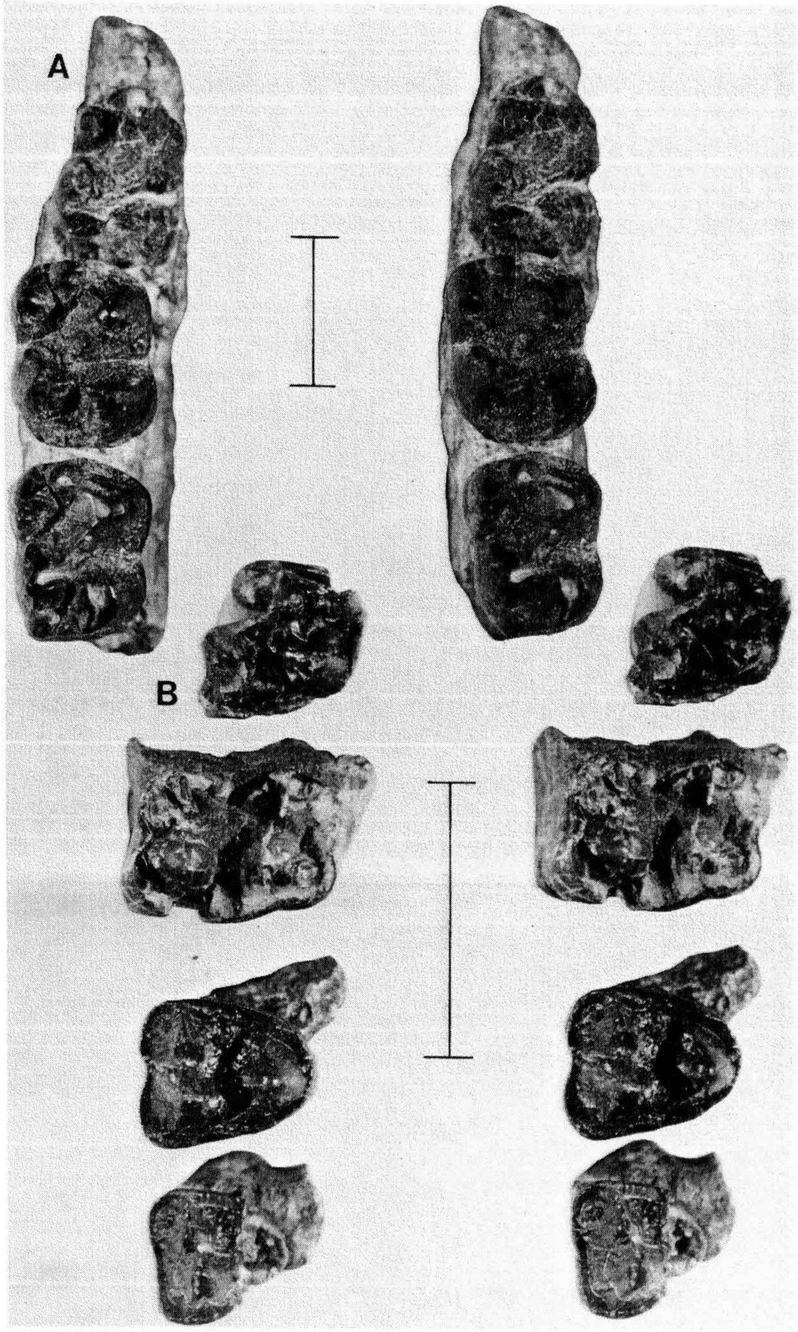
**Holotype**; FMNH P26131, "Hell's Half Acre", DeBeque formation, middle late Paleocene, Mesa County, Colorado.

**Range**: Middle late Paleocene.

**Distribution**: Western Colorado.

**Figure 29.** *Prosthecion major*, stereophotographs. **A.** FMNH P15586, DeBeque formation, western Colorado. Left $M_1$-$M_3$. **B.** FMNH P26131, holotype, DeBeque formation, Western Colorado. Left $P^4$, $M^1$, $M^2$, $M^3$. →

Scale unit represents 1 cm.


A
B

**Diagnosis**: As for the genus.

**Discussion**: *Prosthecion* is known only from one restricted area in western Colorado and is represented by only ten catalogued specimens in the Field Museum of Natural History collection. It is more closely allied with *Ectocion* than with *Phenacodus,* and seemingly represents a separate, perhaps dead-end, branch of the phenacodont radiation (Patterson and West, 1973). No descendants of *Prosthecion* are recognized so at present it plays a decidedly minor role in interpretations of phenacodont history.

## *ECTOCION* Cope, 1882

*Ectocion* Cope, 1882a, Amer. Nat., v. 16, p. 522.

*Gidleyina* Simpson, 1935b, Proc. U.S. Nat. Mus., v. 83, p. 240.

**Type species**: *Ectocion osbornianum,* Graybull beds, Willwood formation, early Wasatchian, Bighorn Basin, Wyoming.

**Included species**: Type plus *E. montanensis, E. wyomingensis, E. superstes* and *E. parvus*.

**Range**: Middle Paleocene to early Eocene.

**Distribution**: Western North America.

**Diagnosis**: Small phenacodont; teeth somewhat lophodont; $P_3$ simple, with high protoconid and weak heel; $P_4$ progressively more molariform with strong entoconid in later species; molar paraconid weak to absent, replaced by lingually sloping paraconid shelf; molar hypoconulid displaced lingually, positioned close to entoconid, upper molars lophodont with strong mesostyle and metacone; metaconule anterior to line between metacone and hypocone.

**Discussion**: Included within *Ectocion* here is material which Simpson (1935b) and Gazin (1956a) considered generically separate as *Gidleyina.* Both, however, noted the close relationship between the two genera and suggested that only one genus might be present. The primary distinction between *Gidleyina* and *Ectocion* was the greater degree of molariformity of the posterior premolars in *Ectocion* and more substantial protocone-paraconule and protocone-metaconule crests in *Gidleyina.* I do not consider these differences substantial enough to justify a generic separation, but they are helpful in recognizing different species of *Ectocion.*

The part of the phenacodont radiation represented by *Ectocion* and *Prosthecion* is quite distinct from the *Phenacodus* lineage, and does not show the prominent increase in size so obvious in *Phenacodus.* The dental specializations of *Ectocion,* lophodonty being the dominant one, suggest that *Ectocion* was exploiting a niche more similar to that of the hyopsodonts than to that of the larger phenacodonts.

### *Ectocion montanensis* (Gidley in Simpson, 1935b, p. 240)
(Figures 30, 32, 39; Table 19)

*Gidleyina montanensis* Gidley in Simpson, 1935b, Proc. U.S. Nat. Mus., v. 83, p. 240.

*Gidleyina silberlingi* Gidley in Simpson, 1935b, Proc. U.S. Nat. Mus., v. 83, p. 240.

*Tetraclaenodon superior* Simpson, 1935b, Proc. U.S. Nat. Mus., v. 83, p. 239.

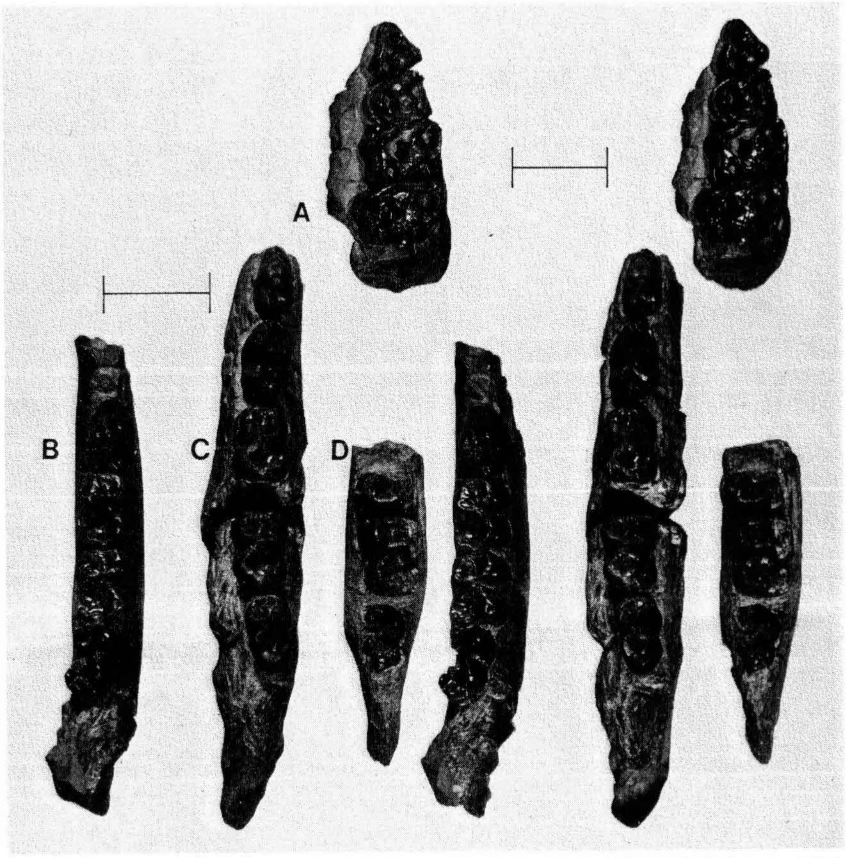


**Figure 30.** *Ectocion montanensis*, stereophotographs. **A.** PU 12048, holotype, Melville formation, Crazy Mountain field, Montana. Left $P^3$-$M^2$. **B.** PU 14603, Melville formation, Crazy Mountain field, Montana. Right $P_4$-$M_3$. **C.** USNM 6166, holotype of *"Gidleyina silberlingi"*, Melville formation, Crazy Mountain field, Montana. Left $P_3$-$M_3$. **D.** USNM 11913, holotype of *"Gidleyina superior"*, Melville formation, Crazy Mountain field, Montana. Left $M_2$-$M_3$.

Scale unit represents 1 cm.

**Holotype**: PU 12048, Loc. 68 (1000 feet above Gidley Quarry), Melville formation, Crazy Mountain Field, Montana.

**Range**: Early late Paleocene.

**Distribution**: Western North America.

**Diagnosis**: Primitive *Ectocion,* with simple premolars. Lower premolars markedly similar to *E. wyomingensis.* Upper $P^3$ with prominent paracone, small connate metacone, no conules; $P^4$ with small metacone, well-developed paraconule, no metaconule. Lower molars with paraconid small but present, enclosing weak trigonid basin hypoconulid more median than in *E. wyomingensis.* Upper molars similar to *E. wyomingensis.*

**Discussion**: *E. montanensis* is the least well known species of *Ectocion,* represented by specimens from the Crazy Mountain Field of Montana (Simpson 1935b, 1937a) and the Black Peaks formation of Texas (Schiebout, 1974). No realistic idea of the range of variation in this species is available (Table 19), but the morphologic characters distinguishing it from *E. wyomingensis* (which was also early Tiffanian but has not yet been found sympatric with *E. montanensis*) seem to be consistent. That *E. montanensis* and *E. wyomingensis* are very closely related is obvious, and the retention of the paraconid in *E. montanensis* places that species in particularly close relationship also to *Tetraclaenodon.*

### *Ectocion wyomingensis* (Gazin, 1956)
(Figures 31, 32, 39; Tables 20, 21)

*Gidleyina wyomingensis* Gazin, 1956a, Smith. Misc. Coll., v. 131, no. 6, p. 42.

**Holotype**: USNM 20790, West End locality, Bison Basin, Ft. Union formation, early Tiffanian, Fremont County, Wyoming.

**Range**: Early Tiffanian.

**Distribution**: Colorado, Wyoming, and Montana.

**Diagnosis**: Premolars simple, similar to *E. montanensis.* Lower molars with reduced paraconid, creating anteriorly open trigonid basin and a lingually sloping paraconid shelf.

**Discussion**: *E. wyomingensis* occupies a morphologically intermediate position between *E. montanensis* with its *Tetraclaenodon*-like lower molars, and *E. osbornianum* with its more complex premolars. All three species are approximately the same size (Tables 19-23). This species can be differentiated from both others only with difficulty and only if adequate specimens are available. Like *E. montanensis,* it has a short temporal range and gave way rather quickly to the more advanced *E. osbornianum.*

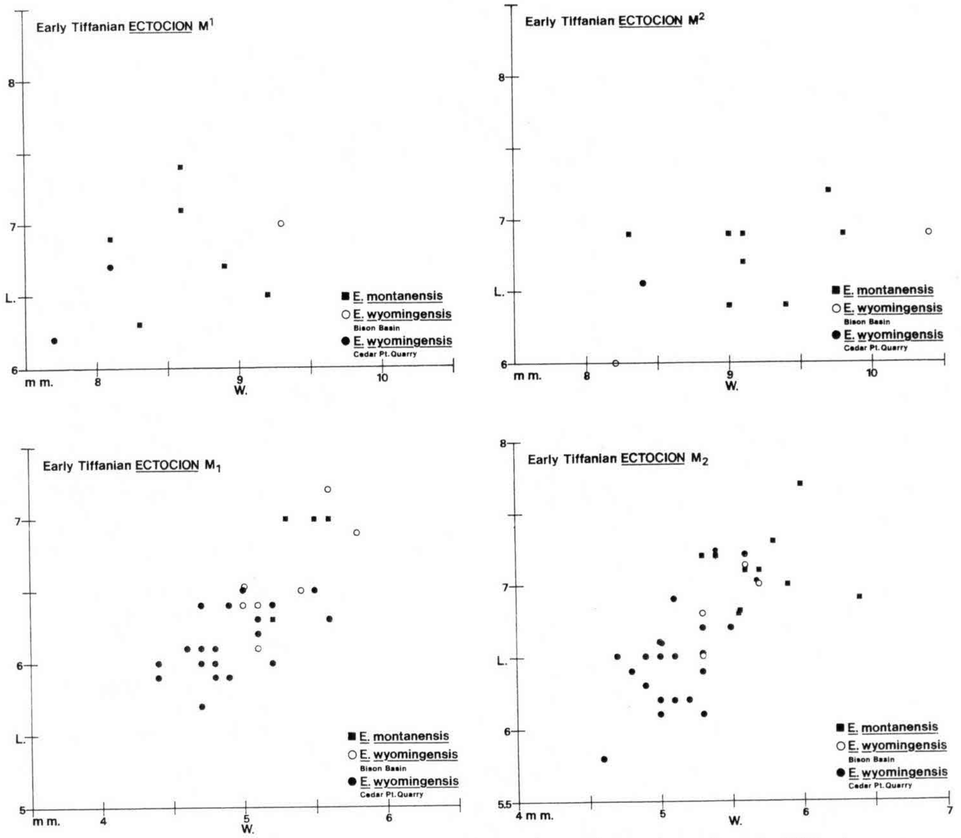


**Figure 31.** Bivariate plots of dimensions of anterior molars of early Tiffanian species of *Ectocion*. Localities as in Table 1.

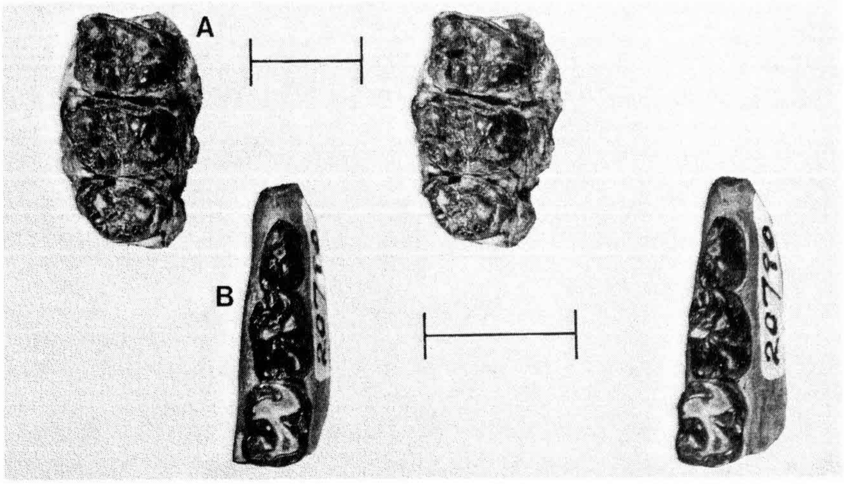


**Figure 32.** *Ectocion wyomingensis,* stereophotographs. **A.** USNM 20795, Fort Union formation, Bison Basin, Wyoming. Right $M^1$-$M^3$. **B.** USNM 20790, holotype, Fort Union formation, Bison Basin, Wyoming. Right $P_3$-$M_1$.
Scale unit represents 1 cm.

### *Ectocion osbornianum* Cope, 1882
### (Figures 33-39; Tables 22, 23)

*Ectocion osbornianum* Cope, 1882c, Proc. Am. Phil. Soc., v. 20, p. 182.

*Ectocion ralstonensis* Granger, 1915, Bull. Am. Mus. Nat. Hist., v. 34, p. 353.

**Holotype**: AMNH 4409, Graybull beds, lower Willwood formation, Wasatchian, Bighorn Basin, Wyoming.

**Range**: Late Paleocene to early Eocene.

**Distribution**: Western North America.

**Diagnosis**: Progressive *Ectocion* with premolars more molariform than in *E. wyomingensis.* $P_4$ with large entoconid, producing marked talonid basin. Molar paraconid virtually absent.

**Figure 33.** *Ectocion osbornianum,* stereophotographs. **A.** PU 20278, Fort Union formation, Silver Coulee beds, Bighorn Basin, Wyoming. Right $P^4$-$M^3$. **B.** PU 17718, Fort Union formation, Silver Coulee beds, Bighorn Basin, Wyoming. Left $P_2$-$M_3$. **C.** USNM 20645, Almy formation, Buckman Hollow, Wyoming. Right $P_4$-$M_2$. **D.** USNM 20736, Almy formation, Buckman Hollow, Wyoming. Right $P_3$-$M_3$.
Scale unit represents 1 cm.

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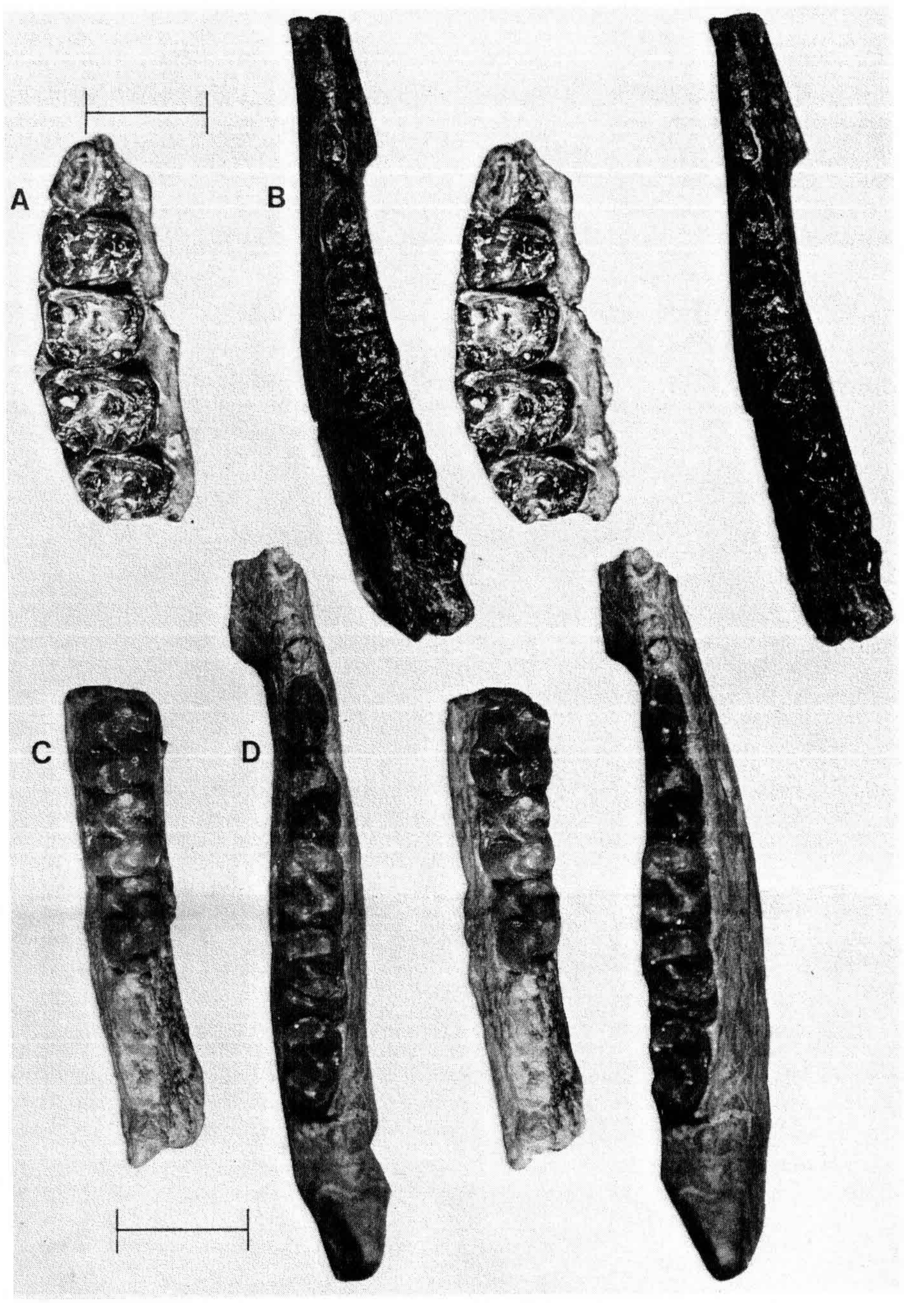
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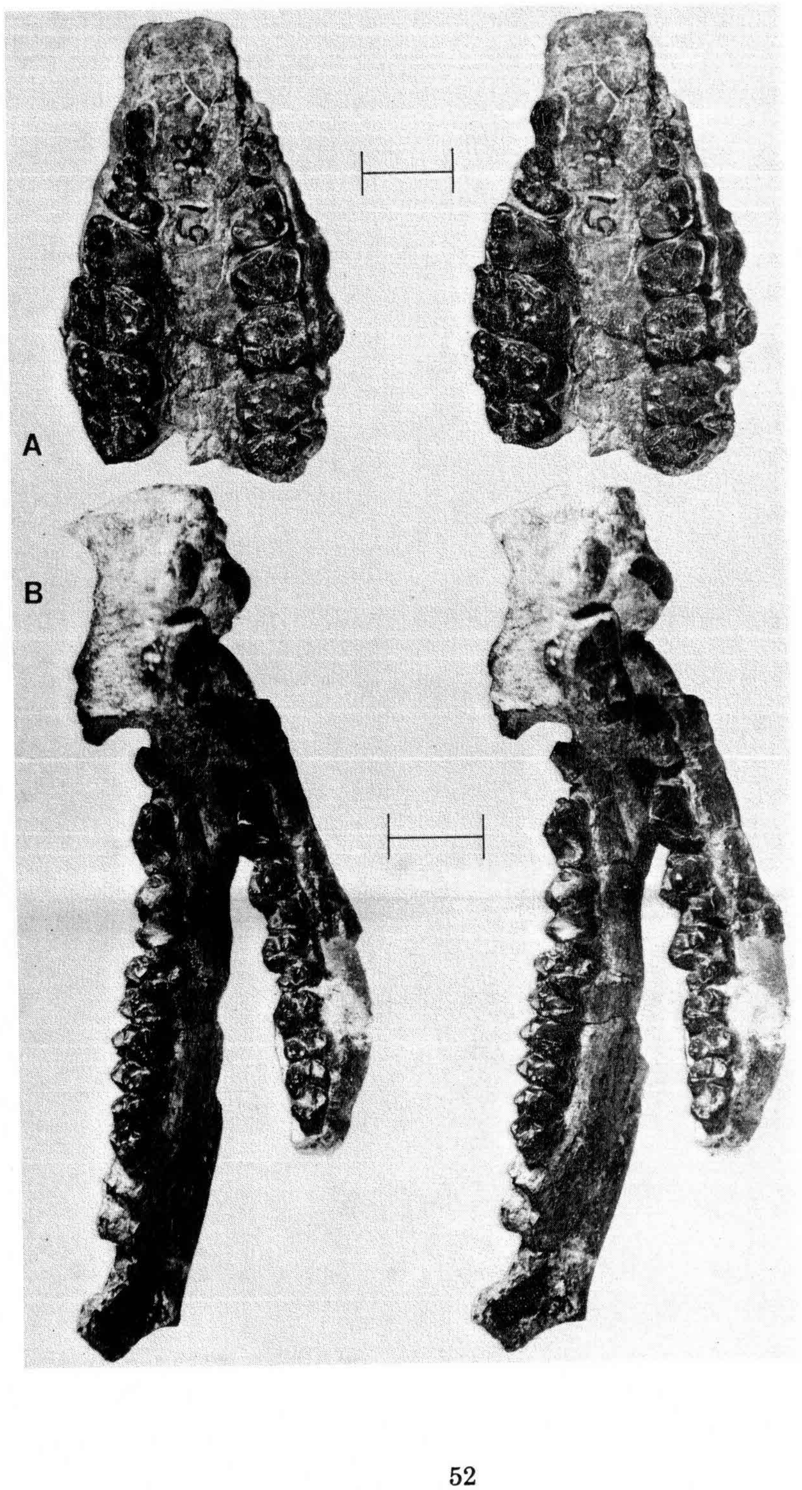
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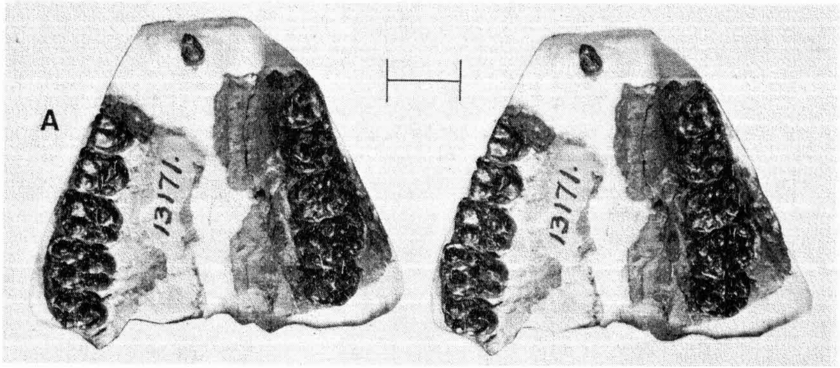


**Figure 35.** *Ectocion osbornianum*, stereophotographs. PU 13171, Willwood formation, Graybull beds, Bighorn Basin, Wyoming. Right and left $P^3$-$M^3$.
Scale unit represents 1 cm.

**Discussion**: Several attempts to arrange latest Paleocene and early Eocene *Ectocion* into different species or lineages have been made in the last several decades (summarized in McKenna, 1960, pp. 101-103, and Delson, 1971, pp. 346-348). The concensus, that a single species is predominant, is completely supported by the numerical data presented here (Tables 22 and 23). I find no significant morphologic or dimensional trends through the range of *E. osbornianum* that will allow recognition of another similar sized species or distinct chronoclines (Simpson, 1943).

### *Ectocion parvus* Granger, 1915
(Figures 37 and 39)

*Ectocion parvus* Granger, 1915, Bull. Am. Mus. Nat. Hist., v. 34, p. 353.

**Holotype**: AMNH 16080, head of Big Sand Coulee, Willwood formation, early Wasatchian, Bighorn Basin, Wyoming.

**Range**: Late Tiffanian to early Wasatchian.

**Distribution**: Wyoming and Colorado.

**Diagnosis**: Smallest *Ectocion* ($M_1$, length 5.5 mm); relatively median hypoconulid on lower molars.

**Discussion**: *E. parvus* is known from the type specimen, a worn mandibular fragment with $M_1$-$M_3$ in place, and three referred specimens (FMNH P15536 from the late Paleocene at DeBeque, western

← **Figure 34.** *Ectocion osbornianum*, stereophotographs. PU 16231, Fort Union formation, Silver Coulee beds, Bighorn Basin, Wyoming. **A.** Palate, right $P^2$, $P^4$-$M^3$; left $P^2$-$M^3$. **B.** Dentaries, right $P_2$-$M_3$; left $P_2$-$M_3$.
Scale unit represents 1 cm.

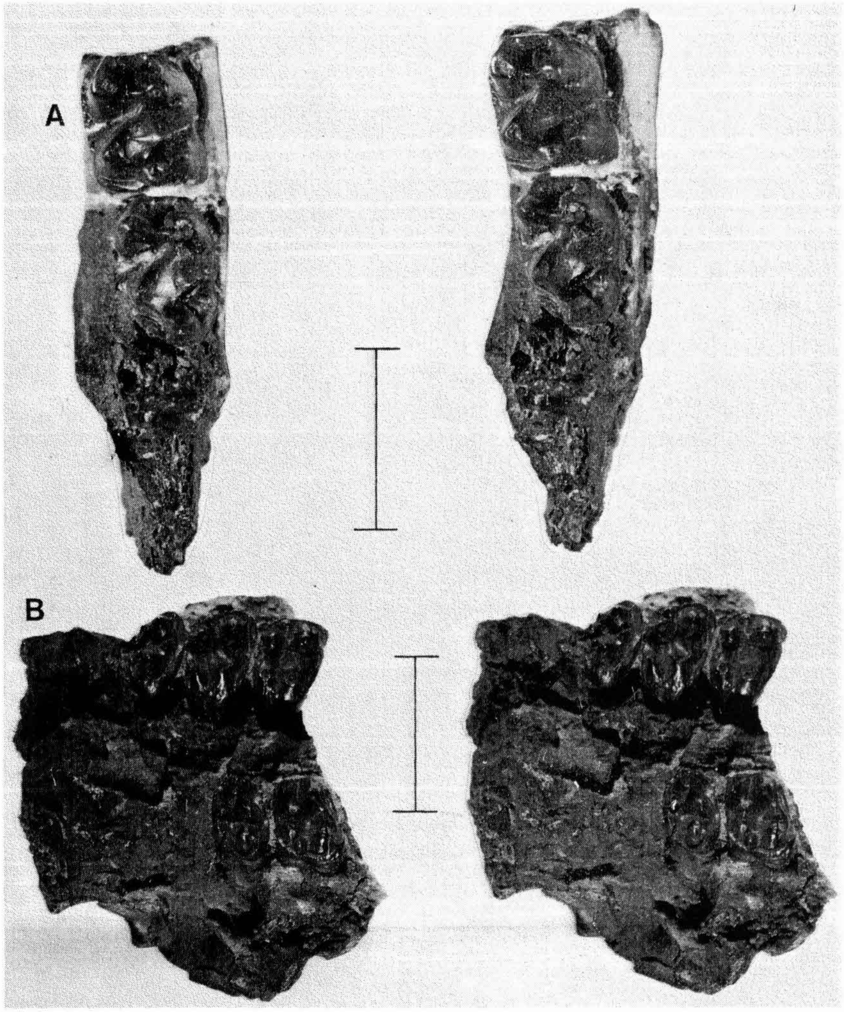


**Figure 36.** *Ectocion osbornianum,* stereophotographs. AMNH 15325, Willwood formation. Graybull beds, Bighorn Basin, Wyoming. **A.** Left $M_2$-$M_3$. **B.** Palate, right $M^1$-$M^3$; left $M^2$-$M^3$.
Scale unit represents 1 cm.

Colorado, and AMNH 57208 and 57286 from the latest Paleocene or earliest Eocene of the Togwotee Pass area, Wyoming [McKenna 1972, p. 87]). It is markedly smaller than any other species of *Ectocion,* the teeth (especially $M_3$) are relatively narrow, and the wear pattern on the posterior flank of the molar metaconid of the holotype is rather unlike more definitive specimens of *Ectocion.* Both

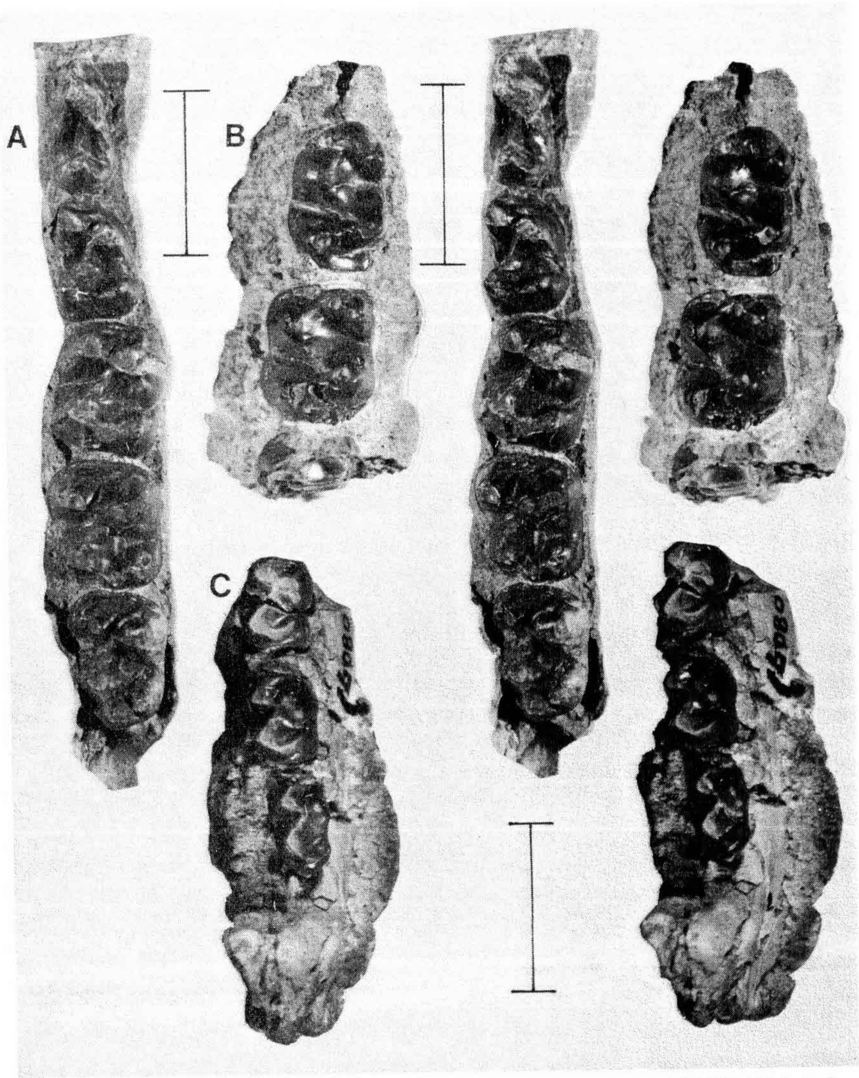
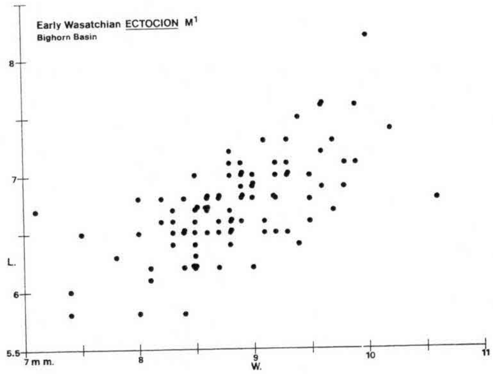
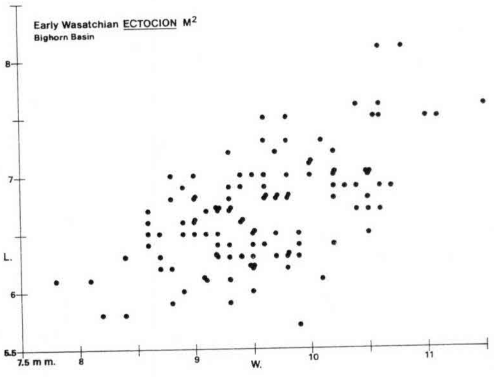
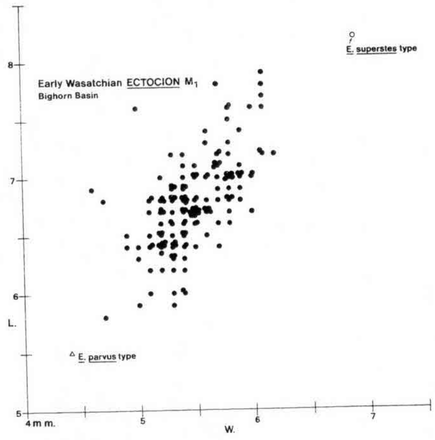


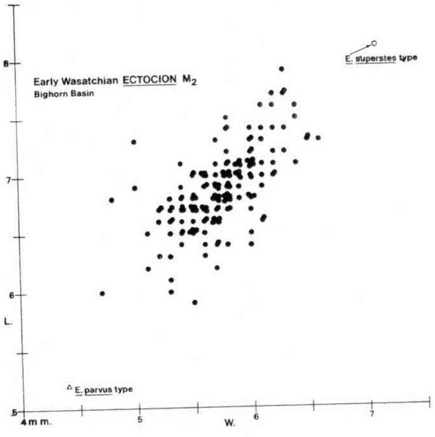
**Figure 37.** *Ectocion,* stereophotographs. **A.** *Ectocion superstes,* AMNH 233A, holotype, Wind River formation. Lost Cabin beds, Wind River Basin, Wyoming. Left $P_3$-$M_3$. **B.** *Ectocion osbornianum,* AMNH 15324, Willwood formation, Graybull beds, Bighorn Basin, Wyoming. Right $M_2$-$M_3$. **C.** *Ectocion parvus,* AMNH 16080, holotype, Willwood formation, Graybull beds, Bighorn Basin, Wyoming, Left $M_1$-$M_3$.

Scale unit represents 1 cm.


Early Wasatchian ECTOCION $M^1$
Bighorn Basin
8
7
L.
6
5.5
7 mm.
8
9
10
11
W.


Early Wasatchian ECTOCION $M^2$
Bighorn Basin
8
7
L.
6
5.5
7.5 mm.
8
9
W.
10
11


E. superstes type
Early Wasatchian ECTOCION $M_1$
Bighorn Basin
8
7
6
L.
E. parvus type
5
4 mm.
5
W.
6
7


E. superstes type
Early Wasatchian ECTOCION $M_2$
Bighorn Basin
8
7
6
L.
E. parvus type
5
4 mm.
5
W.
6
7

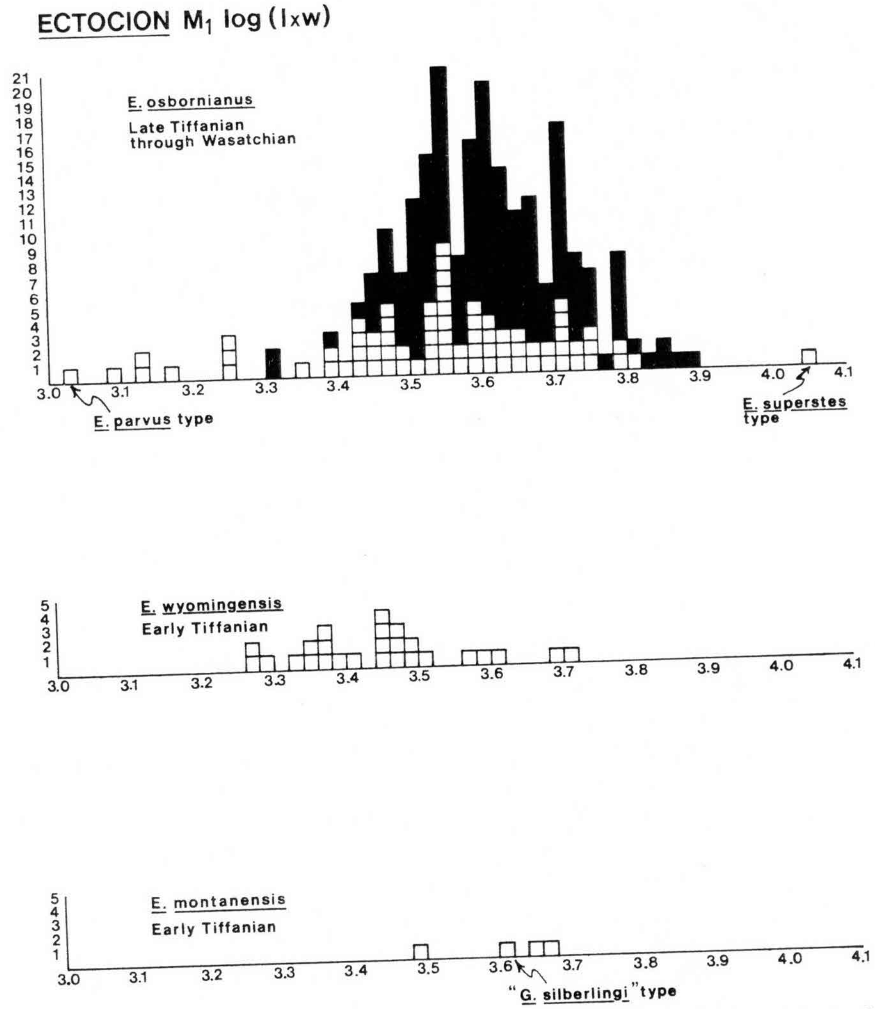


**Figure 39.** Plots of logarithms of the product of length and width measurements of $M_1$ of species of *Ectocion*. In the upper plot, Wasatchian material is indicated by the open squares and late Tiffanian specimens by the solid squares.

← **Figure 38.** Bivariate plots of dimensions of anterior molars of early Wasatchian *Ectocion osbornianum* and *E. parvus* from the Bighorn Basin. The late Wasatchian holotype of *E. superstes* is also indicated.

McKenna (1960, p. 102) and Delson (1971, p. 348) deferred either substantiating the validity of *E. parvus* or subsuming it into another species until a better sample becomes available. In the absence of adequate material, I also merely note the presence of the specimens and the name which has been given to them.

### *Ectocion superstes* Granger, 1915
(Figures 37-39)

*Ectocion superstes* Granger, 1915, Bull. Amer. Mus. Nat. Hist., v. 34, p. 352.

**Holotype**: AMNH 233A, Lost Cabin beds, Wind River formation, late Wasatchian, Wind River Basin, Wyoming.

**Range**: Late Wasatchian.

**Distribution**: Central Wyoming.

**Diagnosis**: Large *Ectocion,* with long $P_3$.

**Discussion**: *E. superstes* is another taxonomic problem. The holotype is the only specimen of *Ectocion* known from post-Graybull rocks; specimens previously referred to *E. superstes* (AMNH 15324 and 15325, both from the early Eocene Willwood formation of the Bighorn Basin, Wyoming) seem better placed in *E. osbornianum.* As with *E. parvus,* attempts have been made to remove AMNH 233A from *Ectocion.* Guthrie (1971, p. 81) suggested that it should be considered a slightly aberrant specimen of *Phenacodus vortmani,* following McKenna (1960, p. 102). I agree with the approach of Delson (1971, p. 349) and tentatively retain *E. superstes* as the largest species of *Ectocion,* represented by only the holotype.

## Evolution in the Phenacodontidae

Relatively little evolutionary change occurred during the fifteen million years of phenacodont history. The earliest genera, *Tetraclaenodon* and *Desmatoclaenus,* had dentitions dominated by low, rounded teeth, small accessory cusps, and simple premolars. *Tetraclaenodon* was also conservative in limb structure, being basically an ambulatory animal (Radinsky, 1966). Trends that can be followed through the Phenacodontidae are of two sorts. In the *Phenacodus* lineage, the cusps remained low and separate, a hypocone was added to $M^3$ and the fourth premolar became more molariform. The canine was reduced in size relative to that of *Tetraclaenodon.* All of these dental changes were in the direction of more efficient crushing of vegetation and a smaller emphasis on shearing. Locomotor elements of *Phenacodus* remained virtually identical to those of *Tetraclaenodon,* indicating rather flexible wrist and ankle structures suited only for moderate speeds.

On the other hand, in the *Ectocion* line, the teeth became progressively more lophodont with the loss of the paraconid and development of a prominent ectoloph as well as cross-lophs. These dental changes enhanced the shearing capabilities of the dentition while reducing the ability for conventional crushing. Radinsky (1966) noted subtle differences between the *Ectocion* astragalus and those of *Tetraclaenodon* and *Phenacodus.* The structure of the *Ectocion* astragulus suggests greater ligamental restriction over lateral movement of the ankle, thus increasing its stability and permitting more rapid movement.

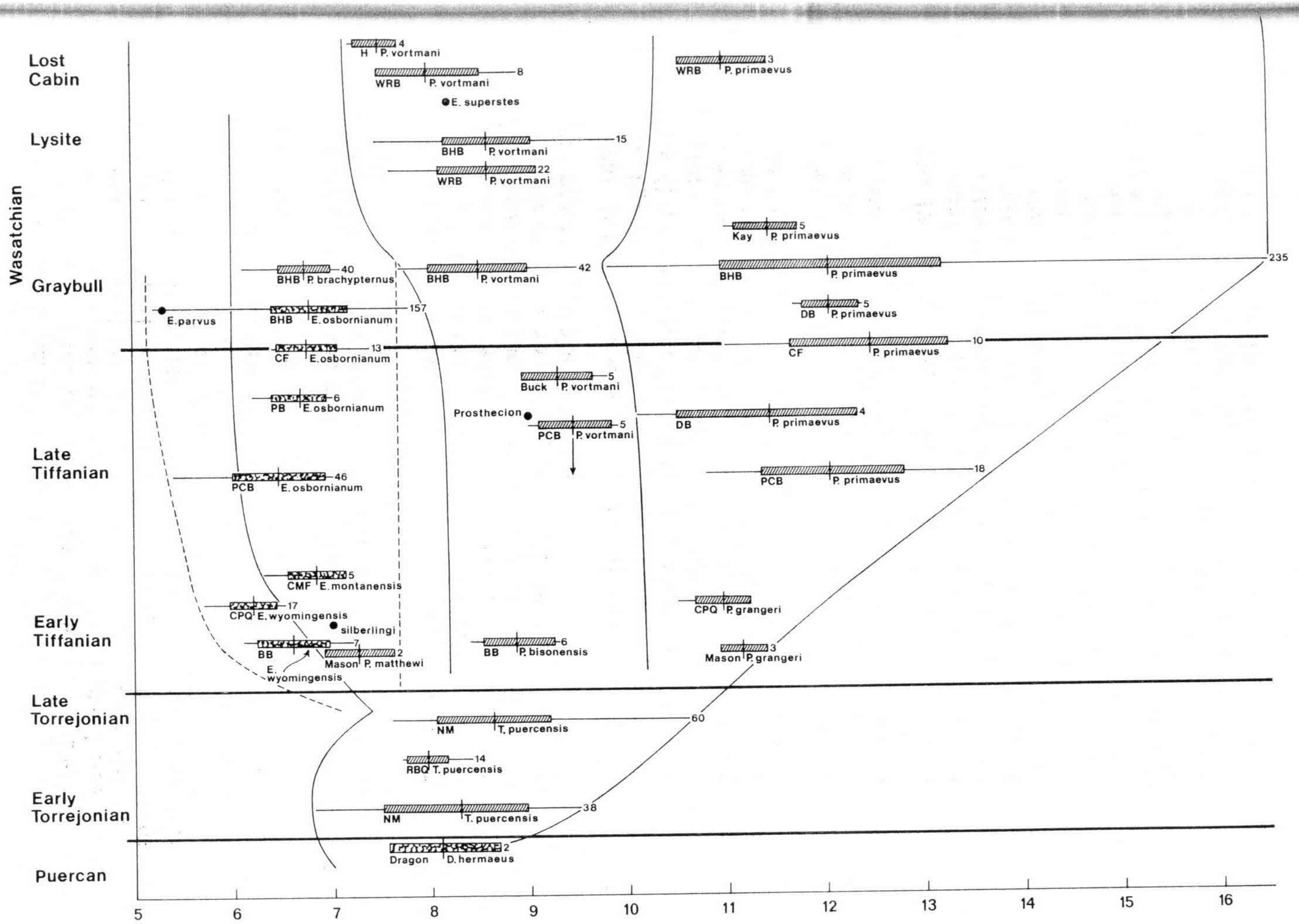
Both the dental and locomotor specializations of *Phenacodus* and *Ectocion* indicate a progressive partitioning of resources available to the phenacodonts.

The basic pattern of phenacodont evolution is shown in figure 40. Starting from *Desmatoclaenus* in the late Puercan, there is a direct progression to the variable *T. puercensis* of the early Torrejonian. This species increased in size through the Torrejonian and apparently gave rise to several species at the end of the Torrejonian and beginning ,of the Tiffanian.

The *Ectocion* line was immediately differentiated into two species, the *Tetraclaenodon*-like *E. montanensis* and the more progressive *E. wyomingensis.* The latter seems to be the most probable ancestor of *E. osbornianum,* the species which dominated in the late Tiffanian and early Wasatchian. The other two Eocene species, *E. parvus* and *E. superstes,* are probably related to *E. osbornianum* in some fashion.

Also related to *Ectocion* is the single species of *Prosthecion. P. major* is, however, at present not aligned with any other phenacodont and does not play a role in phenacodont evolution.

The *Phenacodus* line shows much more complexity than does the *Ectocion* line. In the early Tiffanian three species are present, small *(P. matthewi),* moderate *(P. bisonensis),* and large *(P. grangeri). P. bisonensis* and *P. grangeri* are clearly ancestral to the medium-sized *(P. vortmani)* and large *(P. primaevus)* later species. The possible relationship between *P. matthewi* and *P. brachypternus* is less clear. The elongate premolars of *P. brachypternus* are quite unlike those of *P. matthewi* and actually are more similar to those of *P. vortmani.* Further, there is no small species of *Phenacodus* known from latest Paleocene rocks. *P. brachypternus* appears in the early Eocene with no obvious direct ancestor. Thus there are two potential sources for *P. brachypternus:* 1. a continuation of *P. matthewi,* and 2. a radiation from the *P. vortmani* line at the end of the Paleocene.


Lost Cabin
Lysite
Graybull
Wasatchian
Late Tiffanian
Early Tiffanian
Late Torrejonian
Early Torrejonian
Puercan
H P. vortmani 4
WRB P. vortmani 8
WRB P. primaevus 3
E. superstes
BHB P. vortmani 15
WRB P. vortmani 22
Kay P. primaevus 5
BHB P. brachypternus 40
BHB P. vortmani 42
BHB P. primaevus 235
E. parvus
BHB E. osbornianum 157
DB P. primaevus 5
CF E. osbornianum 13
CF P. primaevus 10
Buck P. vortmani 5
PB E. osbornianum 6
Prosthecion
PCB P. vortmani 5
DB P. primaevus 4
PCB E. osbornianum 46
PCB P. primaevus 18
CMF E. montanensis 5
CPQ E. wyomingensis 17
CPQ P. grangeri
silberlingi
BB 7
Mason P. matthewi 2
E. wyomingensis
BB P. bisonensis 6
Mason P. grangeri 3
NM T. puercensis 60
RBQ T. puercensis 14
NM T. puercensis 38
Dragon D. hermaeus 2
5
6
7
8
9
10
11
12
13
14
15
16

## Extinction

The decline and extinction of phenacodont condylarths in North America is correlated with the early Eocene diversification of a markedly successful descendent family, the Perissodactyla. At the time of most rapid diversification and greatest numerical abundance of the phenacodonts, late Tiffanian and early Wasatchian, the ecologically competitive horses and cursorial rhinoceroses were only just making their first appearances (Radinsky, 1969). Later in the Wasatchian, as the perissodactyls themselves diversified, the phenocodonts diminished in numbers and diversity. It is obvious from both dental patterns and foot structure (Radinsky, 1966) that these two groups occupied the same niches and were in all probability competitors. Van Valen and Sloan (1966, p. 275) quantitatively showed this competition within the early Eocene Four Mile fauna. In accordance with the competitive exclusion principle, the less efficient phenacodonts gave way. By the end of Wasatchian time the transition had, realistically, taken place, even though a few populations of *Phenacodus* persisted into the middle Eocene (West and Atkins, 1970).

## European Phenacodonts

The Phenacodontidae are represented in western Europe by two genera and three species, ranging in age from early Eocene (Sparnacian) to early late Eocene (Lutetian) (Russell, 1968). A revision of the European material is necessary, but is not attempted here; the comments below are all based upon the literature.

*Phenacodus* is represented by two species: *P. teilhardi* (name given by Simpson, 1929, who found that Teilhard's 1927 *P. europaeus* was invalid) which is known from the Sparnacian and Cuisian of France and Belgium, and *P. villaltae* (Crusafont 1956) from the Lutetian of northern Spain. A genus presently restricted to Europe, *Almogaver condali*, is also recognized (Crusafont and Villalta, 1954,

← **Figure 40.** Diagrammatic relationships among the various phenacodonts based upon population samples and unique specimens. Length of the first lower molar is the measurement utilized; the vertical lines represent the mean, the rectangles represent one standard deviation, the horizontal line represents the observed range, and the number indicates the number of specimens measured. The vertical (time) axis is arbitrary. Abbreviations and locality numbers (see Table 1 for details): Dragon—Dragon Canyon (1, 2); NM — New Mexico (4); RBQ — Rock Bench Quarry (5); Mason—Mason Pocket (Tiffany) (10); BB — Bison Basin (13); CPQ — Cedar Point Quarry (14); CMF — Crazy Mountain Field (11); PCB — Polecat Bench (16); DB — DeBeque (27, 46); Buck — Buckman Hollow (Almy) (33); CF — "Clark Fork" (41); BHB — Bighorn Basin (41); Kay — Kay's Locality (Carnegie) (41); WRB — Wind River Basin (48, 52); H — Huerfano Park (50).

1955) from the Spanish Lutetian. Thus *Almogaver* is the youngest known phenacodont, as the Lutetian probably encompasses the early part of the North American Uintan (McKenna et al, 1973).

Rich (1971) made comprehensive comparisons of *P. teilhardi* with *P. primaevus* (as *P. intermedius*), *P. grangeri* (as *Tetraclaenodon transitus)* and *Almogaver condali.* He concluded that there is very little difference between *P. teilhardi* and *P. primaevus,* but did not synonomize the species. Somewhat more substantial differences exist between *P. teilhardi* and the other two taxa, but Rich (p. 55) questioned indirectly the validity of *Almogaver.*

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Table 2. Measurements of Dragon Canyon
*Desmatoclaenus hermaeus*

| TOOTH | DIMENSION | N | X(mm) | s | CV | OR(mm) |
|---|---|---|---|---|---|---|
| $P_4$ | L | 1 | 6.80 | | | |
| | $W_{ant}$ | 1 | 4.50 | | | |
| | $W_{post}$ | 1 | 4.80 | | | |
| $M_1$ | L | 2 | 8.10 | .57 | 6.98 | 7.7- 8.5 |
| | $W_{ant}$ | 2 | 6.50 | .71 | 10.88 | 6.0- 7.0 |
| | $W_{post}$ | 2 | 6.70 | .42 | 6.33 | 6.4- 7.0 |
| $M_2$ | L | 3 | 9.00 | .61 | 6.76 | 8.3- 9.4 |
| | $W_{ant}$ | 3 | 8.50 | .35 | 4.08 | 8.3- 8.9 |
| | $W_{post}$ | 3 | 8.03 | .58 | 7.19 | 7.7- 8.7 |
| $M_3$ | L | 2 | 8.95 | .64 | 7.11 | 8.5- 9.4 |
| | $W_{ant}$ | 2 | 6.42 | 1.03 | 16.08 | 5.7- 7.2 |
| | $W_{post}$ | 2 | 5.31 | .57 | 10.79 | 4.9- 5.7 |
| $P^4$ | L | 1 | 7.20 | | | |
| | W | 1 | 7.80 | | | |
| $M^1$ | L | 1 | 8.20 | | | |
| | $W_{ant}$ | 1 | 10.40 | | | |
| | $W_{post}$ | 1 | 9.60 | | | |
| $M^2$ | L | 4 | 7.80 | .28 | 3.63 | 7.4- 8.0 |
| | $W_{ant}$ | 4 | 11.55 | .58 | 5.02 | 10.8-12.2 |
| | $W_{post}$ | 4 | 10.15 | .35 | 3.37 | 9.8-10.5 |
| $M^3$ | L | 3 | 5.77 | .21 | 3.61 | 5.6- 6.0 |
| | W | 3 | 8.50 | .70 | 8.24 | 8.0- 9.3 |

Table 3. Measurements of
lower Torrejon *Tetraclaenodon puercensis*

| TOOTH | DIMENSION | N | X(mm) | s | CV | OR(mm) |
|---|---|---|---|---|---|---|
| $P_4$ | L | 29 | 8.34 | .88 | 10.55 | 6.0- 9.9 |
| | $W_{ant}$ | 30 | 5.64 | .52 | 9.22 | 4.6- 6.4 |
| | $W_{post}$ | 26 | 5.72 | .62 | 10.84 | 4.3- 6.8 |
| $M_1$ | L | 38 | 8.28 | .78 | 9.44 | 6.8- 9.5 |
| | $W_{ant}$ | 41 | 6.76 | .80 | 11.82 | 5.2- 8.5 |
| | $W_{post}$ | 40 | 6.68 | .80 | 11.97 | 4.4- 8.2 |
| $M_2$ | L | 47 | 8.61 | .77 | 9.00 | 6.6-10.1 |
| | $W_{ant}$ | 45 | 7.34 | .67 | 9.08 | 5.8- 8.7 |
| | $W_{post}$ | 46 | 7.05 | .76 | 10.72 | 5.2- 8.5 |
| $M_3$ | L | 37 | 8.92 | .92 | 10.31 | 6.1-10.7 |
| | $W_{ant}$ | 37 | 6.41 | .54 | 8.45 | 4.9- 7.2 |
| | $W_{post}$ | 36 | 5.49 | .57 | 10.32 | 4.2- 6.5 |
| $P^4$ | L | 15 | 7.34 | .80 | 10.96 | 5.8- 8.4 |
| | W | 16 | 8.43 | .87 | 10.33 | 6.7- 9.8 |
| $M^1$ | L | 24 | 7.62 | .69 | 9.03 | 5.9- 8.8 |
| | $W_{ant}$ | 25 | 9.25 | 1.08 | 11.64 | 7.3-11.2 |
| | $W_{post}$ | 24 | 8.70 | .92 | 10.58 | 6.7- 9.8 |
| $M^2$ | L | 23 | 7.49 | .80 | 10.63 | 6.2- 8.8 |
| | $W_{ant}$ | 23 | 10.10 | 1.01 | 9.97 | 8.0-11.5 |
| | $W_{post}$ | 22 | 8.85 | .87 | 9.81 | 7.0-10.6 |
| $M^3$ | L | 12 | 6.15 | .87 | 14.13 | 4.7- 7.4 |
| | W | 12 | 8.49 | 1.05 | 12.37 | 6.4- 9.5 |

### Table 4. Measurements of Rock Bench Quarry *Tetraclaenodon puercensis*

| TOOTH | DIMENSION | N | X(mm) | s | CV | OR(mm) |
|---|---|---|---|---|---|---|
| $P_4$ | L | 14 | 7.70 | .46 | 5.97 | 7.1- 9.0 |
| | $W_{ant}$ | 13 | 4.90 | .57 | 11.63 | 4.3- 5.9 |
| | $W_{post}$ | 13 | 5.22 | .41 | 7.85 | 4.5- 6.1 |
| $M_1$ | L | 14 | 7.96 | .20 | 2.51 | 7.7- 8.4 |
| | $W_{ant}$ | 15 | 6.35 | .33 | 5.20 | 5.8- 6.9 |
| | $W_{post}$ | 14 | 6.48 | .23 | 3.55 | 6.1- 6.9 |
| $M_2$ | L | 17 | 8.04 | .39 | 4.85 | 7.1- 8.5 |
| | $W_{ant}$ | 17 | 6.98 | 1.00 | 14.33 | 5.9-10.4 |
| | $W_{post}$ | 17 | 6.68 | .72 | 10.78 | 5.6- 7.2 |
| $M_3$ | L | 10 | 8.09 | .61 | 7.54 | 7.0- 9.2 |
| | $W_{ant}$ | 10 | 6.20 | 1.12 | 18.06 | 5.2- 9.1 |
| | $W_{post}$ | 10 | 5.22 | .69 | 13.22 | 4.2- 6.7 |
| $P^4$ | L | 14 | 6.75 | .52 | 7.70 | 5.8- 7.7 |
| | W | 14 | 7.94 | .52 | 6.55 | 6.8- 8.7 |
| $M^1$ | L | 7 | 7.56 | .35 | 4.63 | 7.0- 8.1 |
| | $W_{ant}$ | 7 | 9.84 | .52 | 5.28 | 8.9-10.5 |
| | $W_{post}$ | 7 | 8.97 | .70 | 7.80 | 7.9- 9.7 |
| $M^2$ | L | 12 | 7.43 | .27 | 3.63 | 6.8- 7.8 |
| | $W_{ant}$ | 12 | 10.34 | .88 | 8.51 | 8.5-11.7 |
| | $W_{post}$ | 12 | 8.88 | .75 | 8.45 | 7.5-10.6 |
| $M^3$ | L | 24 | 5.98 | .33 | 5.52 | 5.4- 6.7 |
| | W | 23 | 8.41 | .50 | 5.95 | 7.5- 9.3 |

### Table 5. Measurements of late Torrejon *Tetraclaenodon puercensis*

| TOOTH | DIMENSION | N | X(mm) | s | CV | OR(mm) |
|---|---|---|---|---|---|---|
| $P_4$ | L | 54 | 8.55 | .63 | 7.32 | 7.5-10.1 |
| | $W_{ant}$ | 55 | 6.09 | .86 | 14.05 | 5.1- 9.6 |
| | $W_{post}$ | 50 | 5.79 | .40 | 6.93 | 4.9- 6.6 |
| $M_1$ | L | 60 | 8.63 | .57 | 6.57 | 7.6-10.6 |
| | $W_{ant}$ | 63 | 7.15 | .57 | 8.02 | 6.4-10.1 |
| | $W_{post}$ | 65 | 7.13 | .55 | 7.77 | 6.1- 8.1 |
| $M_2$ | L | 61 | 8.82 | .53 | 6.02 | 7.8- 9.9 |
| | $W_{ant}$ | 63 | 7.79 | .63 | 8.15 | 6.7-10.2 |
| | $W_{post}$ | 63 | 7.34 | .53 | 7.22 | 6.2- 9.0 |
| $M_3$ | L | 71 | 9.02 | .75 | 8.30 | 7.7-10.7 |
| | $W_{ant}$ | 68 | 6.75 | .61 | 9.05 | 5.7- 8.5 |
| | $W_{post}$ | 68 | 5.69 | .47 | 8.34 | 4.9- 7.4 |
| $P^4$ | L | 20 | 7.73 | .58 | 7.53 | 7.0- 8.7 |
| | W | 20 | 8.94 | .92 | 10.30 | 7.6-10.8 |
| $M^1$ | L | 23 | 8.26 | .44 | 5.31 | 7.7- 9.3 |
| | $W_{ant}$ | 22 | 10.19 | .83 | 8.19 | 9.2-11.6 |
| | $W_{post}$ | 23 | 9.61 | .67 | 7.02 | 8.4-10.5 |
| $M^2$ | L | 26 | 8.22 | .51 | 6.16 | 7.3- 9.1 |
| | $W_{ant}$ | 27 | 11.20 | .82 | 7.29 | 9.9-12.8 |
| | $W_{post}$ | 27 | 9.83 | .74 | 7.53 | 8.9-11.4 |
| $M^3$ | L | 22 | 6.53 | .42 | 6.47 | 5.7- 7.5 |
| | W | 22 | 9.09 | .82 | 9.00 | 7.3-10.9 |

## Table 6. Measurements of Mason Pocket *Phenacodus matthewi*

| TOOTH | DIMENSION | N | X(mm) | s | CV | OR(mm) |
|---|---|---|---|---|---|---|
| $P_4$ | L | 2 | 7.40 | .85 | 11.47 | 6.8-8.0 |
| | $W_{ant}$ | 2 | 4.60 | .42 | 9.22 | 4.3-4.9 |
| | $W_{post}$ | 2 | 4.95 | .49 | 10.00 | 4.6-5.3 |
| $M_1$ | L | 2 | 7.25 | .35 | 4.88 | 7.0-7.5 |
| | $W_{ant}$ | 2 | 5.70 | .14 | 2.48 | 5.6-5.8 |
| | $W_{post}$ | 2 | 6.20 | .71 | 11.40 | 5.7-6.7 |
| $M_2$ | L | 2 | 7.50 | .42 | 5.66 | 7.2-7.8 |
| | $W_{ant}$ | 2 | 6.70 | .14 | 2.11 | 6.6-6.8 |
| | $W_{post}$ | 1 | 6.10 | | | |
| $M_3$ | L | 2 | 7.50 | .14 | 1.89 | 7.4-7.6 |
| | $W_{ant}$ | 2 | 5.35 | .35 | 6.61 | 5.1-5.6 |
| | $W_{post}$ | 2 | 5.10 | .14 | 2.77 | 5.0-5.2 |
| $P^4$ | L | | | | | |
| | W | | | | | |
| $M^1$ | L | | | | | |
| | $W_{ant}$ | | | | | |
| | $W_{post}$ | | | | | |
| $M^2$ | L | | | | | |
| | $W_{ant}$ | | | | | |
| | $W_{post}$ | | | | | |
| $M^3$ | L | | | | | |
| | W | | | | | |

## Table 7. Measurements of Bison Basin *Phenacodus bisonensis*

| TOOTH | DIMENSION | N | X(mm) | s | CV | OR(mm) |
|---|---|---|---|---|---|---|
| $P_4$ | L | 5 | 8.72 | .28 | 3.21 | 8.4- 9.0 |
| | $W_{ant}$ | 5 | 5.82 | .31 | 5.33 | 5.3- 6.1 |
| | $W_{post}$ | 5 | 5.78 | .31 | 5.36 | 5.5- 6.2 |
| $M_1$ | L | 7 | 8.89 | .35 | 3.94 | 8.4- 9.3 |
| | $W_{ant}$ | 7 | 6.90 | .50 | 7.25 | 5.9- 7.3 |
| | $W_{post}$ | 7 | 7.20 | .51 | 7.08 | 6.1- 7.6 |
| $M_2$ | L | 4 | 9.45 | .24 | 2.54 | 9.2- 9.7 |
| | $W_{ant}$ | 3 | 7.77 | .49 | 6.35 | 7.2- 8.1 |
| | $W_{post}$ | 4 | 7.55 | .33 | 4.37 | 7.1- 7.9 |
| $M_3$ | L | 3 | 10.50 | .26 | 2.48 | 10.2-10.7 |
| | $W_{ant}$ | 3 | 7.17 | .38 | 5.30 | 6.9- 7.6 |
| | $W_{post}$ | 3 | 6.27 | .30 | 6.06 | 6.0- 6.7 |
| $P^4$ | L | 3 | 7.93 | .55 | 6.94 | 7.3- 8.3 |
| | W | 3 | 8.90 | 1.01 | 11.35 | 7.8- 9.8 |
| $M^1$ | L | 4 | 8.85 | .33 | 3.73 | 8.4- 9.1 |
| | $W_{ant}$ | 3 | 11.20 | .26 | 2.32 | 10.9-11.4 |
| | $W_{post}$ | 4 | 10.08 | .71 | 7.04 | 9.2-10.9 |
| $M^2$ | L | 9 | 9.13 | .56 | 6.13 | 8.3-10.2 |
| | $W_{ant}$ | 7 | 11.50 | 1.08 | 9.39 | 10.0-12.8 |
| | $W_{post}$ | 8 | 10.20 | .92 | 9.02 | 8.9-11.2 |
| $M^3$ | L | 3 | 7.20 | .35 | 4.86 | 7.0- 7.6 |
| | W | 3 | 10.17 | 1.17 | 11.50 | 8.9-11.2 |

Table 8. Measurements of Mason Pocket
*Phenacodus grangeri*

| TOOTH | DIMENSION | N | X(mm) | s | CV | OR(mm) |
|---|---|---|---|---|---|---|
| $P_4$ | L | 3 | 10.33 | .40 | 3.91 | 9.9-10.7 |
| | $W_{ant}$ | 3 | 6.90 | .36 | 5.23 | 6.5- 7.2 |
| | $W_{post}$ | 3 | 7.10 | .26 | 3.73 | 6.8- 7.3 |
| $M_1$ | L | 3 | 11.17 | .21 | 1.86 | 11.0-11.4 |
| | $W_{ant}$ | 3 | 8.80 | .70 | 7.95 | 8.1- 9.5 |
| | $W_{post}$ | 3 | 9.23 | .25 | 2.73 | 9.0- 9.5 |
| $M_2$ | L | 3 | 11.87 | .46 | 3.89 | 11.6-12.4 |
| | $W_{ant}$ | 3 | 10.00 | .60 | 6.00 | 9.4-10.6 |
| | $W_{post}$ | 3 | 9.67 | .40 | 4.18 | 9.3-10.1 |
| $M_3$ | L | 2 | 11.20 | 0 | 0 | 11.2 |
| | $W_{ant}$ | 2 | 8.10 | .07 | 1.05 | 8.1 |
| | $W_{post}$ | 2 | 6.65 | 0 | 0 | 6.6- 6.7 |
| $P^4$ | L | 1 | 10.50 | | | |
| | W | 1 | 11.80 | | | |
| $M^1$ | L | 1 | 9.40 | | | |
| | $W_{ant}$ | 1 | 12.90 | | | |
| | $W_{post}$ | 1 | 12.30 | | | |
| $M^2$ | L | 2 | 11.55 | .92 | 7.96 | 10.9-12.2 |
| | $W_{ant}$ | 2 | 15.70 | 1.56 | 9.91 | 14.6-16.8 |
| | $W_{post}$ | 2 | 14.35 | .92 | 6.41 | 13.7-15.0 |
| $M^3$ | L | 3 | 8.40 | .79 | 9.45 | 7.5- 9.0 |
| | W | 2 | 11.40 | 1.98 | 17.37 | 10.4-12.8 |

Table 9. Measurements of Cedar Point Quarry
*Phenacodus grangeri*

| TOOTH | DIMENSION | N | X(mm) | s | CV | OR(mm) |
|---|---|---|---|---|---|---|
| $P_4$ | L | 4 | 10.68 | .26 | 2.43 | 10.4-10.9 |
| | $W_{ant}$ | 4 | 7.10 | .26 | 3.66 | 6.8- 7.4 |
| | $W_{post}$ | 4 | 7.33 | .47 | 6.41 | 6.9- 8.0 |
| $M_1$ | L | 6 | 10.98 | .26 | 2.37 | 10.5-11.2 |
| | $W_{ant}$ | 6 | 9.02 | .63 | 6.98 | 8.5-10.0 |
| | $W_{post}$ | 6 | 9.50 | .87 | 9.16 | 8.6-10.8 |
| $M_2$ | L | 5 | 10.72 | .24 | 2.24 | 10.4-11.0 |
| | $W_{ant}$ | 5 | 9.24 | .73 | 7.90 | 8.4-10.4 |
| | $W_{post}$ | 5 | 9.38 | .94 | 10.02 | 8.4-11.0 |
| $M_3$ | L | 7 | 11.79 | .99 | 8.40 | 9.7-12.1 |
| | $W_{ant}$ | 7 | 8.03 | .74 | 9.22 | 6.6- 8.7 |
| | $W_{post}$ | 6 | 7.07 | .95 | 13.44 | 5.4- 8.2 |
| $P^4$ | L | 9 | 9.30 | .73 | 7.85 | 7.5- 9.9 |
| | W | 9 | 10.54 | 1.28 | 12.14 | 9.0-12.0 |
| $M^1$ | L | 13 | 10.53 | .64 | 6.08 | 8.8-11.4 |
| | $W_{ant}$ | 13 | 13.50 | .87 | 6.44 | 11.2-14.6 |
| | $W_{post}$ | 13 | 12.94 | .54 | 4.17 | 12.2-13.8 |
| $M^2$ | L | 13 | 10.75 | .65 | 6.05 | 9.4-11.4 |
| | $W_{ant}$ | 13 | 14.58 | .91 | 6.24 | 13.0-16.9 |
| | $W_{post}$ | 11 | 13.19 | .66 | 5.00 | 12.1-14.4 |
| $M^3$ | L | 10 | 8.42 | .72 | 8.55 | 7.5- 9.5 |
| | W | 10 | 12.10 | 1.10 | 9.09 | 9.6-13.6 |

Table 10. Measurements of Bighorn Basin *Phenacodus brachypternus*

| TOOTH | DIMENSION | N | X(mm) | s | CV | OR(mm) |
|---|---|---|---|---|---|---|
| $P_4$ | L | 24 | 7.60 | .41 | 5.40 | 6.7-8.2 |
| | $W_{ant}$ | 23 | 4.11 | .17 | 4.23 | 4.1-5.1 |
| | $W_{post}$ | 23 | 4.52 | .23 | 5.08 | 4.2-5.1 |
| $M_1$ | L | 40 | 6.72 | .26 | 3.89 | 6.1-7.1 |
| | $W_{ant}$ | 38 | 5.34 | .19 | 3.52 | 4.9-5.9 |
| | $W_{post}$ | 38 | 5.35 | .20 | 3.71 | 4.8-5.7 |
| $M_2$ | L | 42 | 6.85 | .24 | 3.48 | 6.4-7.3 |
| | $W_{ant}$ | 43 | 5.65 | .26 | 4.54 | 5.0-6.1 |
| | $W_{post}$ | 42 | 5.45 | .32 | 5.94 | 4.4-6.0 |
| $M_3$ | L | 27 | 7.09 | .38 | 5.36 | 6.3-8.0 |
| | $W_{ant}$ | 27 | 4.79 | .23 | 4.80 | 4.3-5.1 |
| | $W_{post}$ | 27 | 4.30 | .25 | 5.81 | 3.8-4.8 |
| $P^4$ | L | 7 | 6.30 | .39 | 6.22 | 5.7-6.8 |
| | W | 7 | 7.07 | .31 | 4.45 | 6.6-7.4 |
| $M^1$ | L | 16 | 6.66 | .24 | 3.64 | 6.1-7.0 |
| | $W_{ant}$ | 15 | 8.24 | .39 | 4.70 | 7.7-8.8 |
| | $W_{post}$ | 15 | 7.96 | .41 | 5.35 | 7.2-8.3 |
| $M^2$ | L | 13 | 6.35 | .28 | 4.39 | 6.0-6.8 |
| | $W_{ant}$ | 10 | 8.59 | .47 | 5.42 | 8.1-9.5 |
| | $W_{post}$ | 11 | 7.92 | .43 | 5.41 | 7.6-8.9 |
| $M^3$ | L | 11 | 4.95 | .30 | 6.09 | 4.7-5.6 |
| | W | 12 | 6.93 | .48 | 6.92 | 6.2-7.6 |

Table 11. Measurements of Polecat Bench area *Phenacodus vortmani*

| TOOTH | DIMENSION | N | X(mm) | s | CV | OR(mm) |
|---|---|---|---|---|---|---|
| $P_4$ | L | 4 | 9.75 | .34 | 3.50 | 9.4-10.2 |
| | $W_{ant}$ | 4 | 6.08 | .17 | 2.81 | 5.9- 6.3 |
| | $W_{post}$ | 4 | 6.48 | .52 | 8.01 | 5.7- 6.8 |
| $M_1$ | L | 5 | 9.46 | .36 | 3.86 | 9.0- 9.9 |
| | $W_{ant}$ | 5 | 7.36 | .75 | 10.19 | 6.4- 8.0 |
| | $W_{post}$ | 3 | 7.57 | .25 | 3.32 | 7.3- 7.8 |
| $M_2$ | L | 6 | 10.00 | .51 | 5.06 | 9.3-10.7 |
| | $W_{ant}$ | 5 | 8.70 | .39 | 4.53 | 8.3- 9.2 |
| | $W_{post}$ | 5 | 8.12 | .48 | 5.93 | 7.6- 8.8 |
| $M_3$ | L | 9 | 10.21 | .53 | 5.15 | 9.7-11.2 |
| | $W_{ant}$ | 7 | 7.24 | .56 | 7.77 | 6.4- 8.1 |
| | $W_{post}$ | 8 | 6.46 | .58 | 8.91 | 6.0- 7.8 |
| $P^4$ | L | 4 | 8.88 | .13 | 1.42 | 8.7- 9.0 |
| | W | 3 | 9.73 | .06 | .59 | 9.7- 9.8 |
| $M^1$ | L | 4 | 9.25 | .57 | 6.21 | 8.4- 9.6 |
| | $W_{ant}$ | 5 | 10.90 | .55 | 5.07 | 10.0-11.5 |
| | $W_{post}$ | 4 | 10.45 | .17 | 1.59 | 10.2-10.6 |
| $M^2$ | L | 7 | 8.97 | .22 | 2.47 | 8.7- 9.2 |
| | $W_{ant}$ | 7 | 11.51 | .84 | 7.33 | 10.5-13.0 |
| | $W_{post}$ | 7 | 10.56 | .97 | 9.16 | 10.0-12.4 |
| $M^3$ | L | 6 | 7.23 | .42 | 5.78 | 6.7- 7.7 |
| | W | 6 | 10.05 | 1.04 | 10.32 | 8.8-10.9 |

Table 12. Measurements of Buckman Hollow Area *Phenacodus vortmani*

| TOOTH | DIMENSION | N | X(mm) | s | CV | OR(mm) |
|---|---|---|---|---|---|---|
| $P_4$ | L | 5 | 9.52 | .48 | 5.04 | 8.7- 9.9 |
| | $W_{ant}$ | 5 | 6.12 | .61 | 9.97 | 5.6- 6.9 |
| | $W_{post}$ | 5 | 6.12 | .44 | 7.19 | 5.6- 6.7 |
| $M_1$ | L | 5 | 9.30 | .34 | 3.66 | 9.0- 9.8 |
| | $W_{ant}$ | 5 | 7.40 | .41 | 5.54 | 7.0- 8.0 |
| | $W_{post}$ | 5 | 7.44 | .34 | 4.57 | 7.0- 7.8 |
| $M_2$ | L | 3 | 9.80 | .36 | 3.67 | 9.4-10.1 |
| | $W_{ant}$ | 3 | 8.00 | .36 | 4.50 | 7.6- 8.3 |
| | $W_{post}$ | 3 | 7.80 | .36 | 4.62 | 7.4- 8.1 |
| $M_3$ | L | 4 | 10.1 | .40 | 3.96 | 9.9-10.7 |
| | $W_{ant}$ | 4 | 6.85 | .38 | 5.55 | 6.6- 7.4 |
| | $W_{post}$ | 4 | 5.98 | .10 | 1.67 | 5.9- 6.1 |
| $P^4$ | L | 5 | 8.22 | .63 | 7.66 | 7.6- 9.1 |
| | W | 5 | 8.86 | .36 | 4.06 | 8.4- 9.3 |
| $M^1$ | L | 6 | 8.97 | .20 | 2.23 | 8.8- 9.2 |
| | $W_{ant}$ | 6 | 10.55 | .69 | 6.54 | 9.7-11.6 |
| | $W_{post}$ | 6 | 10.38 | .52 | 5.01 | 9.8-10.6 |
| $M^2$ | L | 5 | 9.02 | .31 | 3.44 | 8.6- 9.3 |
| | $W_{ant}$ | 4 | 11.58 | .46 | 3.97 | 11.1-12.2 |
| | $W_{post}$ | 4 | 10.75 | .24 | 2.23 | 10.5-11.0 |
| $M^3$ | L | 6 | 7.48 | .40 | 5.35 | 7.0- 8.1 |
| | W | 6 | 10.00 | .67 | 6.70 | 8.9-10.7 |

Table 13. Measurements of Graybull beds, Willwood formation, Bighorn Basin *Phenacodus vortmani*

| TOOTH | DIMENSION | N | X(mm) | s | CV | OR(mm) |
|---|---|---|---|---|---|---|
| $P_4$ | L | 27 | 8.63 | .47 | 5.44 | 7.9- 9.9 |
| | $W_{ant}$ | 27 | 5.38 | .33 | 6.12 | 4.9- 6.2 |
| | $W_{post}$ | 25 | 5.76 | .39 | 6.80 | 5.2- 6.7 |
| $M_1$ | L | 42 | 8.50 | .51 | 5.99 | 7.7- 9.5 |
| | $W_{ant}$ | 43 | 6.78 | .53 | 8.92 | 6.1- 7.7 |
| | $W_{post}$ | 41 | 6.84 | .50 | 7.28 | 6.0- 7.9 |
| $M_2$ | L | 39 | 8.60 | .54 | 6.28 | 8.1- 9.6 |
| | $W_{ant}$ | 36 | 7.22 | .51 | 8.19 | 6.4- 7.9 |
| | $W_{post}$ | 36 | 6.90 | .55 | 7.97 | 5.8- 7.7 |
| $M_3$ | L | 32 | 8.91 | .72 | 8.05 | 7.8-11.0 |
| | $W_{ant}$ | 31 | 6.20 | .60 | 9.72 | 5.4- 8.2 |
| | $W_{post}$ | 32 | 5.57 | .55 | 9.92 | 4.8- 7.2 |
| $P^4$ | L | 3 | 7.67 | .25 | 3.28 | 7.4- 7.9 |
| | W | 2 | 8.5 | .07 | .87 | 8.1- 8.2 |
| $M^1$ | L | 13 | 8.16 | .39 | 4.84 | 7.5- 8.8 |
| | $W_{ant}$ | 13 | 10.02 | .65 | 6.48 | 9.0-11.0 |
| | $W_{post}$ | 13 | 9.29 | .80 | 8.64 | 8.4-11.0 |
| $M^2$ | L | 13 | 7.76 | .38 | 4.89 | 7.6- 8.4 |
| | $W_{ant}$ | 12 | 10.39 | .76 | 7.29 | 9.5-11.9 |
| | $W_{post}$ | 13 | 9.12 | .98 | 10.72 | 7.8-10.2 |
| $M^3$ | L | 9 | 6.48 | .65 | 9.96 | 5.4- 7.4 |
| | W | 9 | 8.47 | .89 | 10.48 | 7.3- 9.6 |

## Table 14. Measurements of Lysitian, Wind River formation *Phenacodus vortmani*

| TOOTH | DIMENSION | N | X(mm) | s | CV | OR(mm) |
|---|---|---|---|---|---|---|
| $P_4$ | L | 13 | 8.85 | .38 | 4.29 | 8.4- 9.5 |
| | $W_{ant}$ | 12 | 5.58 | .33 | 5.91 | 4.8- 6.0 |
| | $W_{post}$ | 12 | 5.86 | .37 | 6.28 | 5.1- 6.3 |
| $M_1$ | L | 22 | 8.60 | .49 | 5.75 | 7.5- 9.0 |
| | $W_{ant}$ | 22 | 7.08 | .55 | 7.80 | 6.0- 8.0 |
| | $W_{post}$ | 21 | 7.15 | .41 | 5.69 | 6.3- 8.0 |
| $M_2$ | L | 17 | 8.64 | .56 | 6.46 | 7.4- 9.2 |
| | $W_{ant}$ | 17 | 7.38 | .54 | 7.34 | 6.2- 8.3 |
| | $W_{post}$ | 16 | 7.06 | .58 | 8.14 | 5.4- 7.8 |
| $M_3$ | L | 17 | 9.05 | .57 | 6.26 | 7.9-10.1 |
| | $W_{ant}$ | 15 | 6.39 | .51 | 8.01 | 5.7- 7.2 |
| | $W_{post}$ | 15 | 5.64 | .34 | 6.06 | 5.0- 6.0 |
| $P^4$ | L | 7 | 7.51 | .07 | 0.92 | 7.4- 7.6 |
| | W | 7 | 8.79 | .34 | 3.85 | 8.3- 9.3 |
| $M^1$ | L | 7 | 8.10 | .26 | 3.19 | 7.8- 8.5 |
| | $W_{ant}$ | 6 | 10.52 | .43 | 4.10 | 10.0-11.0 |
| | $W_{post}$ | 7 | 9.57 | .49 | 5.14 | 9.0-10.5 |
| $M^2$ | L | 8 | 8.00 | .29 | 3.60 | 7.4- 8.4 |
| | $W_{ant}$ | 8 | 10.98 | .70 | 6.34 | 10.0-11.5 |
| | $W_{post}$ | 8 | 9.53 | .45 | 4.72 | 9.0-10.1 |
| $M^3$ | L | 7 | 6.30 | .36 | 5.65 | 5.8- 6.6 |
| | W | 7 | 8.39 | .89 | 10.63 | 6.7- 9.1 |

## Table 15. Measurements of Lysitian, Willwood formation, Bighorn Basin *Phenacodus vortmani*

| TOOTH | DIMENSION | N | X(mm) | s | CV | OR(mm) |
|---|---|---|---|---|---|---|
| $P_4$ | L | 11 | 8.80 | .47 | 5.31 | 8.0- 9.5 |
| | $W_{ant}$ | 11 | 5.50 | .41 | 7.41 | 4.8- 6.1 |
| | $W_{post}$ | 11 | 5.84 | .41 | 7.03 | 5.2- 6.4 |
| $M_1$ | L | 15 | 8.60 | .46 | 5.40 | 7.4- 9.9 |
| | $W_{ant}$ | 13 | 6.96 | .39 | 5.64 | 5.8- 7.3 |
| | $W_{post}$ | 13 | 7.06 | .44 | 6.27 | 6.1- 7.8 |
| $M_2$ | L | 14 | 8.52 | .48 | 5.64 | 7.6- 9.3 |
| | $W_{ant}$ | 11 | 7.43 | .52 | 6.94 | 6.2- 8.0 |
| | $W_{post}$ | 11 | 7.10 | .44 | 6.27 | 6.1- 7.2 |
| $M_3$ | L | 11 | 8.74 | .83 | 9.45 | 7.4-10.1 |
| | $W_{ant}$ | 10 | 6.32 | .47 | 7.38 | 5.5- 6.8 |
| | $W_{post}$ | 9 | 5.63 | .56 | 9.97 | 4.7- 6.0 |
| $P^4$ | L | 4 | 7.80 | .42 | 5.77 | 7.5- 8.4 |
| | W | 4 | 8.68 | .56 | 6.41 | 8.1- 9.2 |
| $M^1$ | L | 8 | 8.48 | .34 | 4.02 | 8.0- 9.1 |
| | $W_{ant}$ | 6 | 10.73 | .57 | 5.33 | 10.0-11.4 |
| | $W_{post}$ | 7 | 10.00 | .65 | 6.53 | 9.2-11.0 |
| $M^2$ | L | 12 | 8.15 | .41 | 4.98 | 7.4- 8.9 |
| | $W_{ant}$ | 12 | 11.03 | .48 | 4.33 | 10.1-11.7 |
| | $W_{post}$ | 12 | 9.41 | .43 | 4.52 | 8.0-10.1 |
| $M^3$ | L | 8 | 6.96 | .84 | 12.07 | 6.2- 8.1 |
| | W | 8 | 9.26 | 1.30 | 14.07 | 7.8-11.2 |

Table 16. Measurements of Lost Cabin beds, Wind River Formation *Phenacodus vortmani*

| TOOTH | DIMENSION | N | X(mm) | s | CV | OR(mm) |
|---|---|---|---|---|---|---|
| $P_4$ | L | 6 | 8.23 | .39 | 4.78 | 7.5- 8.6 |
| | $W_{ant}$ | 5 | 5.02 | .30 | 6.04 | 4.5- 5.2 |
| | $W_{post}$ | 5 | 5.56 | .35 | 6.31 | 5.2- 6.1 |
| $M_1$ | L | 8 | 8.00 | .52 | 6.44 | 7.5- 8.9 |
| | $W_{ant}$ | 7 | 6.66 | .24 | 3.66 | 6.2- 7.0 |
| | $W_{post}$ | 6 | 6.67 | .22 | 3.24 | 6.4- 7.0 |
| $M_2$ | L | 9 | 8.12 | .36 | 4.43 | 7.7- 8.7 |
| | $W_{ant}$ | 9 | 6.93 | .32 | 4.62 | 6.6- 7.5 |
| | $W_{post}$ | 7 | 6.60 | .30 | 4.55 | 6.2- 7.0 |
| $M_3$ | L | 7 | 8.51 | .45 | 5.23 | 7.8- 9.1 |
| | $W_{ant}$ | 6 | 6.02 | .44 | 7.31 | 5.4- 6.5 |
| | $W_{post}$ | 8 | 5.34 | .49 | 9.12 | 4.6- 6.1 |
| $P^4$ | L | 3 | 7.80 | .62 | 8.01 | 7.3- 8.5 |
| | W | 3 | 8.70 | .20 | 2.30 | 8.5- 8.9 |
| $M^1$ | L | 5 | 8.14 | .54 | 6.59 | 7.7- 8.9 |
| | $W_{ant}$ | 5 | 10.52 | .28 | 2.64 | 10.1-10.8 |
| | $W_{post}$ | 5 | 10.10 | .41 | 4.02 | 9.6-10.5 |
| $M^2$ | L | 2 | 7.60 | .28 | 3.72 | 7.4- 7.8 |
| | $W_{ant}$ | 2 | 10.85 | .35 | 3.26 | 10.6-11.1 |
| | $W_{post}$ | 2 | 9.65 | .21 | 2.20 | 9.5- 9.8 |
| $M^3$ | L | 2 | 6.40 | .14 | 2.21 | 6.3- 6.5 |
| | W | 2 | 8.30 | .14 | 1.70 | 8.2- 8.4 |

Table 17. Measurements of Polecat Bench area *Phenacodus primaevus*

| TOOTH | DIMENSION | N | X(mm) | s | CV | OR(mm) |
|---|---|---|---|---|---|---|
| $P_4$ | L | 25 | 11.37 | .94 | 8.23 | 10.1-12.6 |
| | $W_{ant}$ | 25 | 7.97 | .72 | 9.01 | 6.8- 9.6 |
| | $W_{post}$ | 24 | 8.05 | .57 | 7.07 | 7.4- 9.4 |
| $M_1$ | L | 18 | 12.07 | .71 | 5.87 | 10.8-13.5 |
| | $W_{ant}$ | 17 | 9.72 | .40 | 4.08 | 9.0-10.8 |
| | $W_{post}$ | 17 | 9.74 | .40 | 4.08 | 9.2-10.4 |
| $M_2$ | L | 27 | 12.22 | .78 | 6.41 | 11.0-13.9 |
| | $W_{ant}$ | 26 | 10.58 | .67 | 6.38 | 9.8-12.5 |
| | $W_{post}$ | 28 | 11.11 | .73 | 7.24 | 9.1-12.0 |
| $M_3$ | L | 29 | 12.61 | .97 | 7.71 | 10.0-14.4 |
| | $W_{ant}$ | 27 | 9.16 | .77 | 8.40 | 6.8-10.7 |
| | $W_{post}$ | 28 | 8.09 | .69 | 8.57 | 6.1- 9.2 |
| $P^4$ | L | 8 | 9.96 | .59 | 5.95 | 9.4-11.1 |
| | W | 7 | 11.30 | .64 | 5.64 | 10.6-12.2 |
| $M^1$ | L | 10 | 11.30 | .84 | 7.45 | 10.4-13 |
| | $W_{ant}$ | 9 | 13.51 | 1.18 | 8.70 | 12.3-14.9 |
| | $W_{post}$ | 8 | 13.08 | 1.38 | 10.51 | 11.6-15.4 |
| $M^2$ | L | 26 | 11.15 | .78 | 7.00 | 9.9-13.0 |
| | $W_{ant}$ | 22 | 14.70 | .82 | 5.60 | 13.6-16.6 |
| | $W_{post}$ | 24 | 13.66 | 1.28 | 9.40 | 12.2-16.0 |
| $M^3$ | L | 22 | 9.21 | .92 | 10.00 | 7.3-10.8 |
| | W | 21 | 12.36 | 1.24 | 10.00 | 10.6-14.5 |

Table 18. Measurements of Graybull Beds, Willwood formation, Bighorn Basin *Phenacodus primaevus*

| TOOTH | DIMENSION | N | X(mm) | s | CV | OR(mm) |
|---|---|---|---|---|---|---|
| $P_4$ | L | 157 | 11.65 | 1.04 | 8.92 | 9.2-14.4 |
| | $W_{ant}$ | 155 | 7.78 | .85 | 10.95 | 5.7- 9.4 |
| | $W_{post}$ | 154 | 8.06 | .82 | 10.12 | 6.2-10.1 |
| $M_1$ | L | 235 | 12.04 | 1.09 | 9.08 | 9.8-16.5 |
| | $W_{ant}$ | 220 | 9.84 | .95 | 9.65 | 7.1-13.3 |
| | $W_{post}$ | 221 | 10.10 | 1.04 | 10.31 | 7.1-12.1 |
| $M_2$ | L | 256 | 12.47 | 1.09 | 8.73 | 10.0-15.9 |
| | $W_{ant}$ | 245 | 11.16 | 1.07 | 9.59 | 9.1-13.9 |
| | $W_{post}$ | 241 | 10.75 | 1.10 | 10.20 | 8.7-13.3 |
| $M_3$ | L | 227 | 12.84 | 1.27 | 9.92 | 9.4-15.9 |
| | $W_{ant}$ | 225 | 9.62 | .94 | 9.81 | 6.9-11.9 |
| | $W_{post}$ | 222 | 8.16 | .91 | 11.15 | 5.7-10.2 |
| $P^4$ | L | 71 | 10.37 | .98 | 9.44 | 8.5-12.2 |
| | W | 67 | 11.08 | 1.21 | 10.88 | 8.4-13.2 |
| $M^1$ | L | 101 | 11.52 | .98 | 8.54 | 9.5-13.4 |
| | $W_{ant}$ | 91 | 13.67 | 1.48 | 10.81 | 11.0-17.2 |
| | $W_{post}$ | 89 | 13.43 | 1.50 | 11.16 | 10.6-17.1 |
| $M^2$ | L | 106 | 11.35 | 1.25 | 10.97 | 9.4-12.8 |
| | $W_{ant}$ | 102 | 14.72 | 1.35 | 9.16 | 10.8-17.6 |
| | $W_{post}$ | 101 | 13.66 | 1.41 | 10.32 | 10.8-17.6 |
| $M^3$ | L | 109 | 9.75 | .99 | 10.18 | 7.9-12.3 |
| | W | 103 | 12.63 | 1.24 | 9.82 | 10.1-15.4 |

Table 19. Measurements of Fort Union formation, Melville beds, late Paleocene, Douglass Quarry *Ectocion montanensis*

| TOOTH | DIMENSION | N | X(mm) | s | CV | OR(mm) |
|---|---|---|---|---|---|---|
| $P_4$ | L | 5 | 6.66 | .33 | 4.95 | 6.4-7.2 |
| | $W_{ant}$ | 5 | 4.50 | .19 | 4.22 | 4.2-4.7 |
| | $W_{post}$ | 5 | 4.44 | .21 | 4.73 | 4.2-4.7 |
| $M_1$ | L | 5 | 6.82 | .30 | 4.40 | 6.3-7.0 |
| | $W_{ant}$ | 4 | 5.20 | .28 | 5.38 | 4.8-5.4 |
| | $W_{post}$ | 3 | 5.43 | .21 | 3.87 | 5.2-5.6 |
| $M_2$ | L | 6 | 6.98 | .19 | 2.72 | 6.8-7.3 |
| | $W_{ant}$ | 6 | 5.83 | .30 | 5.15 | 5.6-6.4 |
| | $W_{post}$ | 6 | 5.47 | .19 | 3.47 | 5.3-5.8 |
| $M_3$ | L | 4 | 7.35 | .39 | 5.31 | 7.0-7.9 |
| | $W_{ant}$ | 3 | 4.87 | .25 | 5.17 | 4.6-5.1 |
| | $W_{post}$ | 3 | 4.13 | .15 | 3.63 | 4.0-4.3 |
| $P^4$ | L | 3 | 5.90 | .66 | 11.19 | 5.3-6.6 |
| | W | 3 | 6.87 | .40 | 5.82 | 6.4-7.1 |
| $M^1$ | L | 6 | 6.82 | .40 | 5.87 | 6.3-7.4 |
| | $W_{ant}$ | 6 | 8.62 | .40 | 4.64 | 8.1-9.2 |
| | $W_{post}$ | 6 | 7.73 | .31 | 4.01 | 7.4-8.1 |
| $M^2$ | L | 9 | 6.71 | .34 | 5.07 | 6.1-7.2 |
| | $W_{ant}$ | 8 | 9.18 | .47 | 5.12 | 8.3-9.8 |
| | $W_{post}$ | 8 | 7.80 | .35 | 4.49 | 7.3-8.2 |
| $M^3$ | L | 5 | 5.50 | .16 | 2.91 | 5.3-5.7 |
| | W | 5 | 7.86 | .40 | 5.09 | 7.3-8.4 |

Table 20. Measurements of Fort Union formation, late Paleocene, Bison Basin *Ectocion wyomingensis*

| TOOTH | DIMENSION | N | X(mm) | s | CV | OR(mm) |
|---|---|---|---|---|---|---|
| $P_4$ | L | 5 | 6.48 | .33 | 5.09 | 6.0- 6.8 |
| | $W_{ant}$ | 5 | 4.48 | .36 | 8.04 | 4.1- 4.9 |
| | $W_{post}$ | 5 | 4.38 | .39 | 8.90 | 4.0- 4.9 |
| $M_1$ | L | 7 | 6.57 | .36 | 5.48 | 6.1- 7.2 |
| | $W_{ant}$ | 7 | 5.07 | .25 | 4.93 | 4.7- 5.4 |
| | $W_{post}$ | 7 | 5.27 | .33 | 6.26 | 5.0- 5.8 |
| $M_2$ | L | 4 | 6.85 | .26 | 3.80 | 6.5- 7.1 |
| | $W_{ant}$ | 4 | 5.48 | .21 | 3.83 | 5.3- 5.7 |
| | $W_{post}$ | 4 | 5.28 | .22 | 4.17 | 5.2- 5.5 |
| $M_3$ | L | 4 | 7.45 | .38 | 5.10 | 6.9- 7.7 |
| | $W_{ant}$ | 4 | 4.90 | .32 | 6.53 | 4.5- 5.2 |
| | $W_{post}$ | 4 | 4.40 | .18 | 4.09 | 4.2- 4.6 |
| $P^4$ | L | 1 | 6.9 | | | |
| | W | 1 | 7.6 | | | |
| $M^1$ | L | 1 | 7.0 | | | |
| | $W_{ant}$ | 1 | 9.3 | | | |
| | $W_{post}$ | 1 | 8.9 | | | |
| $M^2$ | L | 2 | 6.45 | .64 | 9.92 | 6.0- 6.9 |
| | $W_{ant}$ | 2 | 9.30 | 1.56 | 16.77 | 8.2-10.4 |
| | $W_{post}$ | 2 | 8.15 | .78 | 9.57 | 7.6- 8.7 |
| $M^3$ | L | 3 | 5.10 | .20 | 3.92 | 4.9- 5.3 |
| | W | 3 | 7.50 | .93 | 12.27 | 6.5- 8.3 |

Table 21. Measurements of Fort Union formation, Late Paleocene, Cedar Point Quarry *Ectocion wyomingensis*

| TOOTH | DIMENSION | N | X(mm) | s | CV | OR(mm) |
|---|---|---|---|---|---|---|
| $P_4$ | L | 9 | 6.30 | .33 | 5.24 | 5.8-6.6 |
| | $W_{ant}$ | 9 | 3.93 | .23 | 5.85 | 3.5-4.2 |
| | $W_{post}$ | 9 | 3.98 | .22 | 5.53 | 3.6-4.3 |
| $M_1$ | L | 17 | 6.17 | .23 | 3.73 | 5.7-6.5 |
| | $W_{ant}$ | 16 | 4.57 | .24 | 5.25 | 4.2-5.1 |
| | $W_{post}$ | 18 | 4.88 | .35 | 7.17 | 4.4-5.6 |
| $M_2$ | L | 21 | 6.52 | .35 | 5.37 | 5.8-7.2 |
| | $W_{ant}$ | 21 | 5.06 | .31 | 6.13 | 4.6-5.6 |
| | $W_{post}$ | 20 | 4.97 | .35 | 7.04 | 4.2-5.5 |
| $M_3$ | L | 12 | 7.00 | .31 | 4.43 | 6.7-7.7 |
| | $W_{ant}$ | 12 | 4.43 | .38 | 8.58 | 3.5-5.0 |
| | $W_{post}$ | 12 | 4.10 | .35 | 8.54 | 3.3-4.5 |
| $P^4$ | L | 3 | 5.77 | .12 | 2.08 | 5.7-5.9 |
| | W | 3 | 6.87 | .35 | 5.09 | 6.5-7.2 |
| $M^1$ | L | 2 | 6.45 | .35 | 5.43 | 6.2-6.7 |
| | $W_{ant}$ | 2 | 7.90 | .28 | 3.54 | 7.7-8.1 |
| | $W_{post}$ | 2 | 7.10 | .28 | 3.94 | 6.9-7.3 |
| $M^2$ | L | 1 | 6.60 | | | |
| | $W_{ant}$ | 1 | 8.40 | | | |
| | $W_{post}$ | 1 | 7.50 | | | |
| $M^3$ | L | 3 | 5.10 | .26 | 5.10 | 4.8-5.3 |
| | W | 3 | 7.57 | .49 | 6.47 | 7.0-7.9 |

Table 22. Measurements of Ft. Union formation, late Paleocene, Polecat Bench area *Ectocion osbornianum*

| TOOTH | DIMENSION | N | X(mm) | s | CV | OR(mm) |
|---|---|---|---|---|---|---|
| $P_4$ | L | 23 | 6.57 | .63 | 9.65 | 5.8- 7.7 |
| | $W_{ant}$ | 25 | 4.33 | .47 | 10.76 | 3.6- 5.0 |
| | $W_{post}$ | 25 | 4.48 | .46 | 10.21 | 3.6- 5.2 |
| $M_1$ | L | 46 | 6.43 | .46 | 7.19 | 5.4- 7.0 |
| | $W_{ant}$ | 48 | 5.08 | .52 | 10.25 | 4.3- 5.9 |
| | $W_{post}$ | 47 | 5.22 | .52 | 9.97 | 3.7- 6.1 |
| $M_2$ | L | 42 | 6.62 | .42 | 6.29 | 5.7- 7.3 |
| | $W_{ant}$ | 43 | 5.39 | .43 | 6.81 | 4.5- 6.1 |
| | $W_{post}$ | 43 | 5.15 | .38 | 7.40 | 4.3- 5.8 |
| $M_3$ | L | 32 | 7.11 | .54 | 7.55 | 6.1- 8.2 |
| | $W_{ant}$ | 31 | 4.63 | .38 | 8.21 | 3.9- 5.2 |
| | $W_{post}$ | 30 | 4.12 | .36 | 8.76 | 3.3- 4.7 |
| $P^4$ | L | 17 | 6.35 | .44 | 6.93 | 5.4- 7.5 |
| | W | 16 | 7.63 | .56 | 7.28 | 6.4- 8.6 |
| $M^1$ | L | 24 | 6.65 | .36 | 5.34 | 5.8- 7.3 |
| | $W_{ant}$ | 22 | 8.81 | .61 | 6.97 | 8.1- 9.8 |
| | $W_{post}$ | 22 | 8.05 | .62 | 7.75 | 7.1- 8.9 |
| $M^2$ | L | 31 | 6.61 | .50 | 7.58 | 5.8- 7.7 |
| | $W_{ant}$ | 30 | 9.37 | .60 | 6.45 | 7.8-10.8 |
| | $W_{post}$ | 28 | 8.29 | .66 | 7.93 | 6.7- 9.5 |
| $M^3$ | L | 22 | 5.23 | .32 | 6.06 | 4.8- 6.1 |
| | W | 22 | 7.65 | .55 | 7.18 | 6.9- 8.7 |

Table 23. Measurements of Bighorn Basin, Willwood formation, Graybull Beds, early Wasatchian *Ectocion osbornianum*

| TOOTH | DIMENSION | N | X(mm) | s | CV | OR(mm) |
|---|---|---|---|---|---|---|
| $P_4$ | L | 95 | 6.99 | .51 | 7.27 | 5.8- 8.0 |
| | $W_{ant}$ | 91 | 4.60 | .31 | 6.77 | 3.8- 5.3 |
| | $W_{post}$ | 91 | 4.78 | .36 | 7.45 | 4.0- 5.6 |
| $M_1$ | L | 157 | 6.77 | .39 | 5.78 | 5.2- 7.8 |
| | $W_{ant}$ | 157 | 5.39 | .33 | 6.11 | 3.8- 6.1 |
| | $W_{post}$ | 156 | 5.42 | .31 | 5.81 | 4.6- 6.2 |
| $M_2$ | L | 162 | 6.87 | .36 | 5.24 | 5.9- 8.0 |
| | $W_{ant}$ | 158 | 5.72 | .35 | 6.13 | 4.7- 6.6 |
| | $W_{post}$ | 156 | 5.44 | .32 | 5.85 | 4.5- 6.1 |
| $M_3$ | L | 103 | 7.32 | .49 | 6.65 | 6.4- 8.6 |
| | $W_{ant}$ | 111 | 4.91 | .34 | 6.83 | 4.0- 5.8 |
| | $W_{post}$ | 110 | 4.42 | .53 | 12.04 | 3.7- 5.5 |
| $P^4$ | L | 48 | 6.48 | .40 | 6.11 | 5.8- 7.8 |
| | W | 48 | 7.65 | .63 | 8.23 | 5.5- 8.8 |
| $M^1$ | L | 95 | 6.73 | .41 | 6.08 | 5.8- 8.2 |
| | $W_{ant}$ | 94 | 8.84 | .62 | 6.98 | 7.1-10.6 |
| | $W_{post}$ | 93 | 8.31 | .60 | 7.19 | 7.0-10.0 |
| $M^2$ | L | 111 | 6.67 | .43 | 6.42 | 5.7- 8.1 |
| | $W_{ant}$ | 108 | 9.53 | .65 | 6.79 | 8.2-11.1 |
| | $W_{post}$ | 108 | 8.54 | .60 | 6.99 | 6.0-10.0 |
| $M^3$ | L | 63 | 5.55 | .43 | 7.78 | 4.7- 6.9 |
| | W | 62 | 8.08 | .54 | 6.63 | 6.6- 9.8 |