EVOLUTION OF PALEOCENE AND EOCENE PHENACODONTIDAE (MAMMALIA, CONDYLARTHRA)

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PAPERS ON PALEONTOLOGY—RECENT NUMBERS

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ABSTRACT

The family Phenacodontidae (Condylarthra, Mammalia) occurs in the Paleocene and Eocene of North America and Europe. North American phenacodontids are among the most abundant mammals during their range from middle Torrejonian (63 Ma) through Bridgerian land-mammal ages (49 Ma). In Europe, phenacodontids are rare and known only from early and middle Eocene deposits.

This study evaluates the pattern of evolution, and the geographic and chronologic distribution of phenacodontid taxa, and investigates some causal factors for these patterns.

Phenacodontid evolution is analyzed on the basis of more than 6,000 dental phenacodontid specimens. Torrejonian phenacodontids are *Tetraclaenodon puercensis* and *T. septentrionalis* (new species). Phenacodontids restricted to the Tiffanian are: *Ectocion collinus, E. cedrus* (new species), *E. mediotuber* (new species), *Phenacodus matthewi, P. bisonensis, P. grangeri,* and *P. magnus* (new species). *Phenacodus vortmani* ranges from late Tiffanian through Bridgerian. *Ectocion major* is restricted to the Clarkforkian. *Ectocion osbornianus, E. parvus, Copecion brachypternus,* and *P. intermedius* occur in Clarkforkian and Wasatchian. *C. davisi* and *P. trilobatus* are only known from the Wasatchian. *E. superstes* and *P. intermedius* are known from the Bridgerian. European Eocene phenacodontids are *P. teilhardi, P. lemoinei* (new species), and *P. condali.*

The distribution of phenacodontid taxa is partly determined by the sedimentary facies in which fossils occur, which suggests habitat specialization for several phenacodontid taxa. This is most obvious in the late Tiffanian: *E. cedrus* and *P. magnus* dominate in poorly-drained environments, while *E. mediotuber, P. vortmani,* and *P. grangeri* dominate in well-drained environments.

Nondental evidence is rare for phenacodontids. Two well preserved *Phenacodus* skulls and a fragmentary *Ectocion* skull are described here. Sexual dimorphism characterizes both genera. *Ectocion* is dimorphic in the size of the canines, and *Phenacodus* has paranasal sinuses inflated in one of the sexes.

Fragmentary skeletons of *Copecion* and *Ectocion* indicate that these taxa are more cursorial than *Phenacodus,* though all phenacodontids show cursorial specializations.

I
INTRODUCTION

The Paleocene and early Eocene was a time of great importance in mammalian evolution. In the late Cretaceous mammals were generally small and unspecialized, while by the end of the Eocene mammals reached the range of morphological and size diversity that they display today. The 30 million year interval between the end of the Cretaceous and the end of the Eocene is characterized by a rapid turnover of groups, with rapid increases and decreases in abundance.

Phenacodontidae are not members of the first diversification of North American Paleocene mammals. *Tetraclaenodon*, the oldest phenacodontid, appeared in the Torrejonian land-mammal age, approximately 63 million years ago, two million years after the beginning of the Paleocene. Once phenacodontids appeared, they did enjoy success in numbers: in late Torrejonian, Tiffanian, and Clarkforkian land-mammal ages they are among the most abundant North American mammals. But in the Wasatchian land-mammal age new groups were introduced and phenacodontids dwindled in importance. Final extinction in the Bridgerian land-mammal age at approximately 49 million years ago is only a pseudo-extinction according to conventional wisdom, because potential descendants of phenacodontids, Perissodactyla, are still with us (Radinsky, 1966).

The importance of phenacodontids for paleontology is due in part to their great numbers. The database compiled for this study contains information on more than 6,000 phenacodontid fossils. The size of the sample and my attempt to quantify morphological traits make it possible to quantitatively verify many qualitative observations. The large database also allows the use of statistical techniques that are helpful only with large sample sizes.

Phenacodontids are represented in most paleontological collections in North America, and most students of vertebrate paleontology have been introduced to *Phenacodus* as a model of an "ancestral ungulate." A maxilla of *Phenacodus* was the first vertebrate fossil ever collected in North America by humans. The specimen (AMNH 32661) was found by native Americans in what is now called New Mexico, probably between 700 and 900 A.D. (Simpson, 1942).

Phenacodontids are among the best known fossil mammals since Cope's (1885) description of a skull and skeleton. As a result, the group is featured in many evolutionary scenarios and Phenacodontidae forms the foundation of the mammalian order Condylarthra Cope, 1881. This order is probably paraphyletic and possibly polyphyletic, but it has formed a convenient heuristic grouping for the ancestors of many mammalian orders, including Artiodactyla, Perissodactyla, Cetacea, and Proboscidea (Simpson, 1945; Van Valen, 1978).

Several authors have published reviews of Phenacodontidae. Cope (1884, 1885) devoted many pages to their systematics and anatomy, and Granger (1915) revised the systematics of phenacodontids then known. Matthew (1937) discussed *Tetraclaenodon* in detail, and Simpson reviewed both *Phenacodus* (1937c) and *Ectocion* (1943). The most recent review of phenacodontids was published by West (1976).

Several developments make a new study necessary: collections have vastly increased over the past ten years, and study of local stratigraphy has added a detailed time dimension to evolutionary patterns and processes. On a broader scale, the biochronological framework for the Paleocene and early Eocene of western North America has improved (Gingerich, 1976a; Schankler, 1980; Gingerich, 1983; Archibald et al., 1987). Thus phenacodontid evolution can be traced on the basis of large, stratigraphically controlled samples. Few authors have described skeletal remains of phenacodontids, although relatively complete specimens are available. Description of all known osteological material is necessary before phenacodontid morphology can be evaluated for questions dealing with the higher phylogeny of mammals.

In Chapter II, I will summarize the biochronological framework that I have used, and discuss the localities where phenacodontid fossil have been found. In Chapter III, I will describe the taxa that comprise phenacodontids, using mainly dental evidence. Chapter IV discusses the pattern of phenacodontid evolution and investigates some of its causes. Chapter V describes the cranial anatomy of phenacodontids, and Chapter VI discusses some postcranial material. Chapter VII summarizes a few important aspects of the previous chapters. Appendix I gives summary statistics for a number of dental variables of important Paleocene and Eocene phenacodontid populations.

IDENTIFICATION AND MEASUREMENT

The main purpose of this work is to describe phenacodontid dental and cranial morphology, to document an-

1

agenesis, and to propose a lower level classification for the family Phenacodontidae.

Examination of phenacodontid specimens included measuring a number of standard dimensions of canines and cheek teeth. Calipers were used for measuring at a precision of 0.1 millimeters, and measurements are reported in mm. From two to seven measurements were taken on investigated teeth (Fig. 1). Only teeth not damaged or worn in the parts relevant to the measurement were measured. Length and width measurements were taken parallel or perpendicular to the long axis of the tooth. Height measurements were taken from the dentine-enamel junction to the tip of the crown, perpendicular to this junction.

Length and width were measured of C_1, P_2-M_3, D_{3-4}, C^1, P^2-M^3, and D^{3-4}. Height of the protoconid was measured in the canines and P_2. In P_3, P_4, D_3, and D_4, the heights of the protoconid and metaconid were determined. In P_4 and D_4 two distances relating to the length of the trigonid basin were measured. These were the distance between the anterior side of the tooth and the tips of protoconid and metaconid respectively. In addition the distance between protoconid and metaconid was measured, perpendicular to the long axis of the tooth.

Widths of the trigonid and talonid were measured on all lower molars perpendicular to the long axis of the tooth. Where not specified in the rest of the text, I will use the trigonid width as the measure for "width of a lower molar." Length and width of the trigonid basin were measured parallel and perpendicular to the long axis of the tooth respectively on all lower molars. On M_2 and M_3, I also measured the height of the protoconid and the distance between hypoconid and hypoconulid. On D^4 and the upper molars, I measured the three dimensional distance between the tips of paracone and parastyle, while on upper molars the height of the mesostyle above the cingulum was also determined.

In addition to the measurements, discrete characters were scored on every specimen. These included the presence or absence of an entoconid on P_4, the orientation of the paracristid on the lower molars, the presence or absence of a metaconule on P^4, and the presence or absence of a lingual cingulum on the upper molars.

These measurements and scores, and some information on provenance and identity of a specimen were entered in a computer database. Rows in this database represent more than 6,000 phenacodontid specimens, and more than 100 columns give quantitative and qualitative information about each specimen. There is no specimen in which all rows are filled, because there is no phenacodontid specimen in which all permanent and deciduous teeth are preserved in perfect condition. The fragmentary nature of most of the studied fossils caused missing data to prevail in most rows.

The computer file was used to identify quantitative differences between clusters of phenacodontids in Chapter III, and it also served as an independent quantitative check on morphological observations. Apparent diagnostic characteristics, such as the elongation of the trigonid basin, were often quantified as a ratio of two dimensions and compared numerically. Summary statistics for the more conventional measurements of large samples of phenacodontids are listed in Appendix I. Where relevant, measurements or combinations of measurements are cited in the text.

Statistical description of morphological differences was usually critical because differences are often small and hard to describe qualitatively. On the other hand, the studied morphologies were usually similar enough to allow easy recognition of homologous points and quantification.

A variety of statistical methods was used to investigate aspects of morphology. The University of Michigan main frame statistical software package MIDAS was used for most calculations. If not mentioned otherwise, differences were considered significant when p-values were equal to or smaller than 0.05.

The main purpose of Chapter III is to describe the differences between the phenacodontid taxa, as an aid in identification of phenacodontids by future workers. I have tried to describe differences in the simplest possible way. Linear dimensions distinguish well between different phenacodontids and can be studied even for fragmentary specimens. The natural logarithms of linear measures such as length and width are studied in order to make the variance of samples independent of their mean (Bryant, 1986). Ratios can often be used to describe simple shape differences and can be calculated on fragmentary material.

More complicated analyses such as principal component analysis and discriminant function analysis are only used when simpler methods do not distinguish adequately between taxa. The disadvantage of these methods is that only relatively complete specimens can be used. Scores in principal component analysis cannot be calculated without the original dataset available, and this method is thus less useful to identify specimens by future workers who do not have the data set of the present analysis. Discriminant function analysis will yield functions on the basis of which unknown specimens can be identified, but this method can only be used when two groups can be distinguished unambiguously before the analysis is done (such in the analysis of *Ectocion cedrus* and *E. parvus*).

Once lineages were identified, evolution was studied within each lineage. Quantification is imperative for the documentation of anagenesis. The database of dental phenacodontid measurements was critical in testing apparent observed changes. Dental remains are far more common than skeletal remains and are therefore the main source of information for this analysis. The largest samples from single time planes, as well as the longest sequence of adjacent time planes is from the Clarks Fork and central Bighorn Basins (approximately 4,500 specimens in my analysis). The stratigraphic record for the Paleocene and early Eocene is relatively complete and fossils from this area can be studied against a more or less continuous time axis. Suitable names were available for most of the recognized phenacodontid lineages, but new names are proposed for some
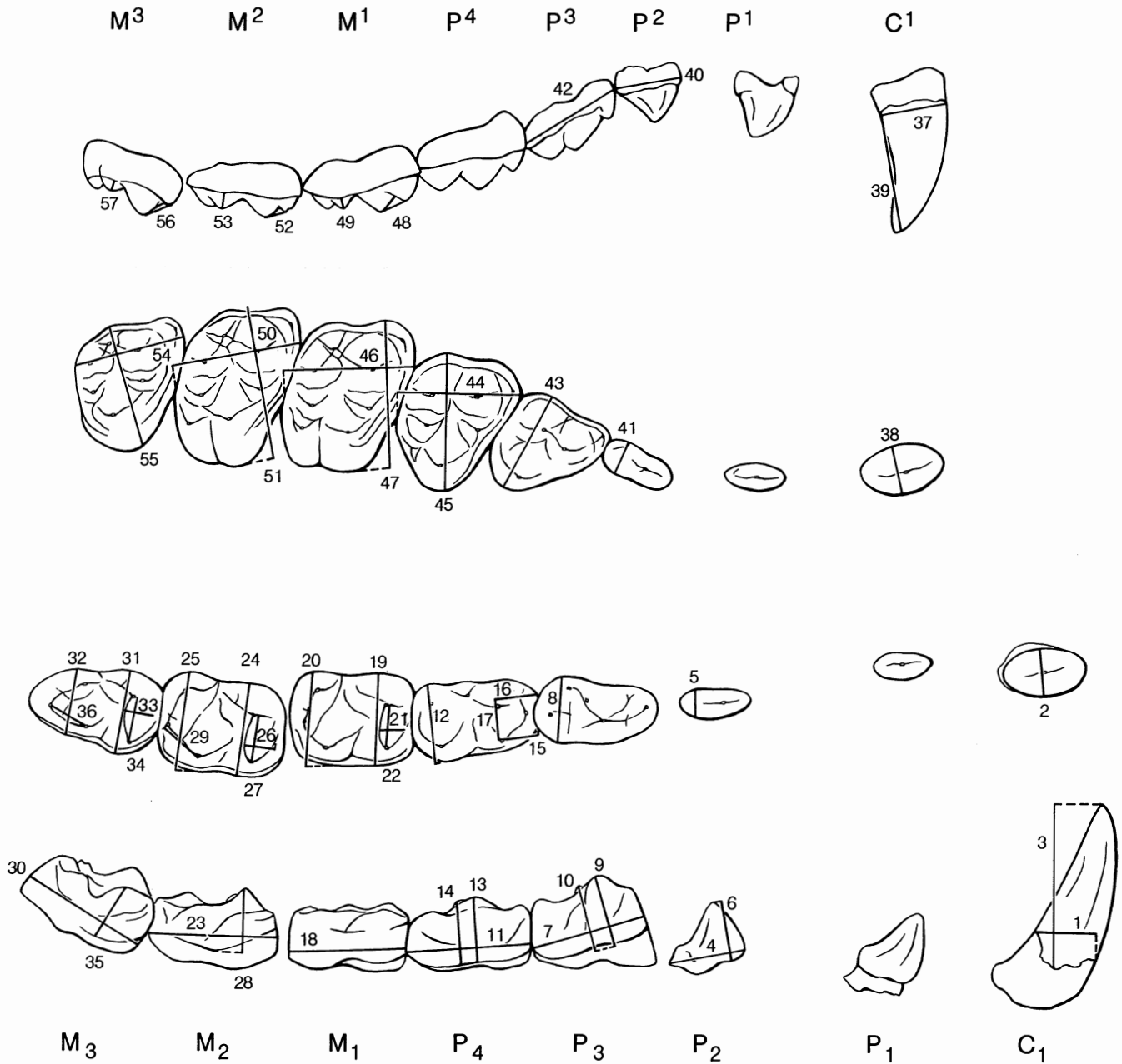
Figure 1. Method of measuring phenacodontid teeth. 1, C_1 length; 2, C_1 width; 3, C_1 height; 4, P_2 length; 5, P_2 width; 6, P_2 height; 7, P_3 length; 8, P_3 width; 9, protoconid height of P_3; 10, metaconid height of P_3; 11, P_4 length; 12, P_4 width; 13, protoconid height of P_4; 14, metaconid height of P_4; 15, distance between protoconid and anterior extremity of P_4; 16, distance between metaconid and anterior extremity of P_4; 17, distance between protoconid and metaconid of P_4; 18, M_1 length; 19, M_1 trigonid width; 20, M_1 talonid width; 21, M_1 trigonid basin length; 22, M_1 trigonid basin width; 23, M_2 length; 24, M_2 trigonid width; 25, M_2 talonid width; 26, M_2 trigonid basin length; 27, M_2 trigonid basin width; 28, M_2 protoconid height; 29, distance between hypoconid and hypoconulid of M_2; 30, M_3 length; 31, M_3 trigonid width; 32, M_3 talonid width; 33, M_3 trigonid basin length; 34, M_3 trigonid basin width; 35, M_3 protoconid height; 36, distance between hypoconid and hypoconulid of M_3; 37, C^1 length; 38, C^1 width; 39, C^1 height; 40, P^2 length; 41, P^2 width; 42, P^3 length; 43, P^3 width; 44, P^4 length; 45, P^4 width; 46, M^1 length; 47, M^1 width; 48, distance between paracone and parastyle of M^1; 49, height of mesostyle of M^1; 50, M^2 length; 51, M^2 width; 52, distance between paracone and parastyle of M^2; 53, height of mesostyle of M^2; 54, M^3 length; 55, M^3 width; 56, distance between paracone and parastyle of M^3; 57, height of mesostyle of M^3.

lineages. I will refer to the named lineage segments as taxa, except where new names are proposed. They could also be called "species" or "operational taxonomic units." Wiley (1981:65) describes similarity of ecophenotypes as the most important criterion for the recognition of allopatric taxa. Gingerich (1976a, 1976b) and Bown and Rose (1987) have discussed the recognition of taxa in the fossil record. Similarities used to define taxa can be primitive or derived, the only constraint is that the taxa are morphologically homogeneous.

Anatomical nomenclature follows the English translations of the Nomina Anatomica Veterinaria as cited in Miller's Anatomy of the Dog (Evans and Christensen, 1979) where possible.

Institutional abbreviations

North America:

ACM	Amherst College, Amherst, Massachusetts.
AMNH	American Museum of Natural History, New York, New York.
CCM	Carter County Museum, Ekalaka, Montana.
CM	Carnegie Museum of Natural History, Pittsburgh, Pennsylvania.
DMNH	Denver Museum of Natural History, Denver, Colorado.
FMNH	Field Museum of Natural History, Chicago, Illinois.
KU	Kansas University, Lawrence, Kansas.
MCZ	Museum of Comparative Zoology, Harvard University, Boston, Massachusetts.
NMC	National Museum of Canada, Ottawa, Ontario.
PU	Princeton University, Princeton, New Jersey (one specimen, exhibited in the Department of Geology).
TMM-TAMU	Texas Memorial Museum, Texas A&M University, Austin, Texas.
UA	University of Alberta, Edmonton, Alberta.
UCM	University of Colorado, Boulder, Colorado.
UCMP	University of California, Berkeley, California.
UM	University of Michigan, Museum of Paleontology, Ann Arbor, Michigan.
USGS	U. S. Geological Survey, Denver, Colorado.
USNM	United States National Museum, Smithsonian Institution, Washington, D. C.
UW	University of Wyoming, Laramie, Wyoming.
YPM	Yale University, Peabody Museum, New Haven, Connecticut.
YPM-PU	Yale University, Peabody Museum, Princeton Collection, New Haven, Connecticut.

Europe:

IRSNB	Institut Royale des Sciences Naturelles de Belgique, Brussels, Belgium.
MNHN	Muséum National d'Histoire Naturelle, Paris, France.

Specimens from the collections of several European amateurs were studied. These are identified by the following suffixes:

Bn	collection of Dr. J. Braillon.
Lo	collection of Mr. P. Louis.
Md	collection of Mr. M. Duchamplecheval.
Wo	collection of Mr. G. Wouters.

II
GEOCHRONOLOGY AND LOCALITIES

Phenacodontids are mainly known from North America, although a few specimens of *Phenacodus* have been recovered in Europe. No definite phenacodontids are known from other continents. One molar constitutes the hypodigm of South American Paleocene *Andinodus*, which was considered a phenacodontid or didolodontid by de Muizon and Marshall (1987) and Marshall and de Muizon (1988). Simpson (1978) noted resemblances between South American *Perutherium* and phenacodontids, but stopped short of including *Perutherium* in Phenacodontidae. Following Van Valen (1988), I do not consider these taxa phenacodontids. *Paraphenacodus* was described on the basis of two molars from the Eocene of Asia (Gabunia, 1971). The narrow trigonid of these molars is unlike a phenacodontid, and the morphology of P_4 and M_3 in a newly discovered dentary from the Zaisan Basin definitely differs from typical phenacodontids. Russell and Zhai (1987) considered this taxon an artiodactyl of uncertain familial affinities. Van Valen (1978) included Indo-Pakistani *Pilgrimella* in phenacodontids but did not give reasons for this inclusion. Wells and Gingerich (1983) have shown that *Pilgrimella* is an anthracobunid. Chinese Paleogene deposits have yielded a few unpublished dentary fragments that have been interpreted as phenacodontid (McKenna, pers. comm., 1989).

NORTH AMERICAN BIOCHRONOLOGY AND LOCALITIES

Early Paleogene continental sediments of North America are mainly found in the intermontane basins of the eastern Rocky Mountains (Fig. 2). The chronology of these deposits is firmly established thanks to continuous interest of paleontologists and geologists, and is summarized by Archibald et al. (1987), and Krishtalka et al. (1987). The generally accepted Torrejonian, Tiffanian, Clarkforkian, and Wasatchian land-mammal ages have been subdivided into biochrons. The full names for the biochrons are summarized in Table 1. I will use shortened forms of these (names before slash mark) from here on.

I follow the zonation of Torrejonian, Tiffanian, and Clarkforkian biochrons as summarized by Archibald et al. (1987), including the three-fold division of the Torrejonian. Gingerich (1976a) proposed an additional terminal Torrejonian zone, based on the presence of *Pantolambda cavirictum* and *Pronothodectes jepi*. This zone may prove to be a useful biostratigraphical tool when more late Torre-

jonian localities become known, but can at present only be recognized at a few localities (Archibald et al., 1987).

For the Wasatchian, I follow the zonation proposed by Schankler (1980) and Gingerich (1983) for the Bighorn Basin, with a few minor additions and changes in nomenclature. Schankler's (1980) zones were mainly based on faunal turnovers and may be artifacts of sampling to some degree (Badgley and Gingerich, 1988), but they form a useful tool until the biochronology of the Wasatchian is better studied.

The earliest Wasatchian *Cantius torresi* Lineage-Zone is added to Schankler's (1980) zonation. This zone is described in detail by Gingerich (1989) as "Wa_0" (Wasatchian zero). In order to be consistent with the nomenclature applied to other zones, I prefer naming it for a published taxon restricted to it (*Cantius torresi* Gingerich, 1986). Based on the occurrence of the phenacodontid *Copecion davisi*, this zone can now also be recognized in the Powder River Basin, which gives it more than local importance (see Chapter III).

Schankler (1980) divided the early Wasatchian into two biochrons, terminated by faunal turnovers called Biohorizon A and B. He called the biochrons the Lower and Upper *Haplomylus-Ectocion* zones. These names are an unfortunate choice because both taxa used in naming also occur in the Clarkforkian, and because they do not indicate the difference between the Lower and Upper *Haplomylus-Ectocion* zones (which is the faunal turnover). In the interest of stability I will not propose new names for these biochrons, but this will be necessary when the common taxa of the early Wasatchian (especially the perissodactyls) are revised. The Lower *Haplomylus-Ectocion* zone coincides with the Sandcouleean of Granger (1914; see also Gingerich, 1983).

Schankler (1980) proposed the name "*Bunophorus* Interval-Zone" for the time period after the extinction of 13 taxa from the Upper *Haplomylus-Ectocion* zone, but before the appearance of *Heptodon* and *Vulpavus canavus*. According to Schankler (1980) and Bown (pers. comm., 1988) the name of the zone does not completely overlap with the range of the taxon after which it is named, because *Bunophorus* actually appears before the faunal turnover. In addition to this, Krishtalka and Stucky (1985) have expanded the range of *Bunophorus* into the *Haplomylus-Ectocion* zone by including a taxon formerly referred to *Diacodexis* in it. I will here use the *Bunophorus etsagicus/Heptodon*
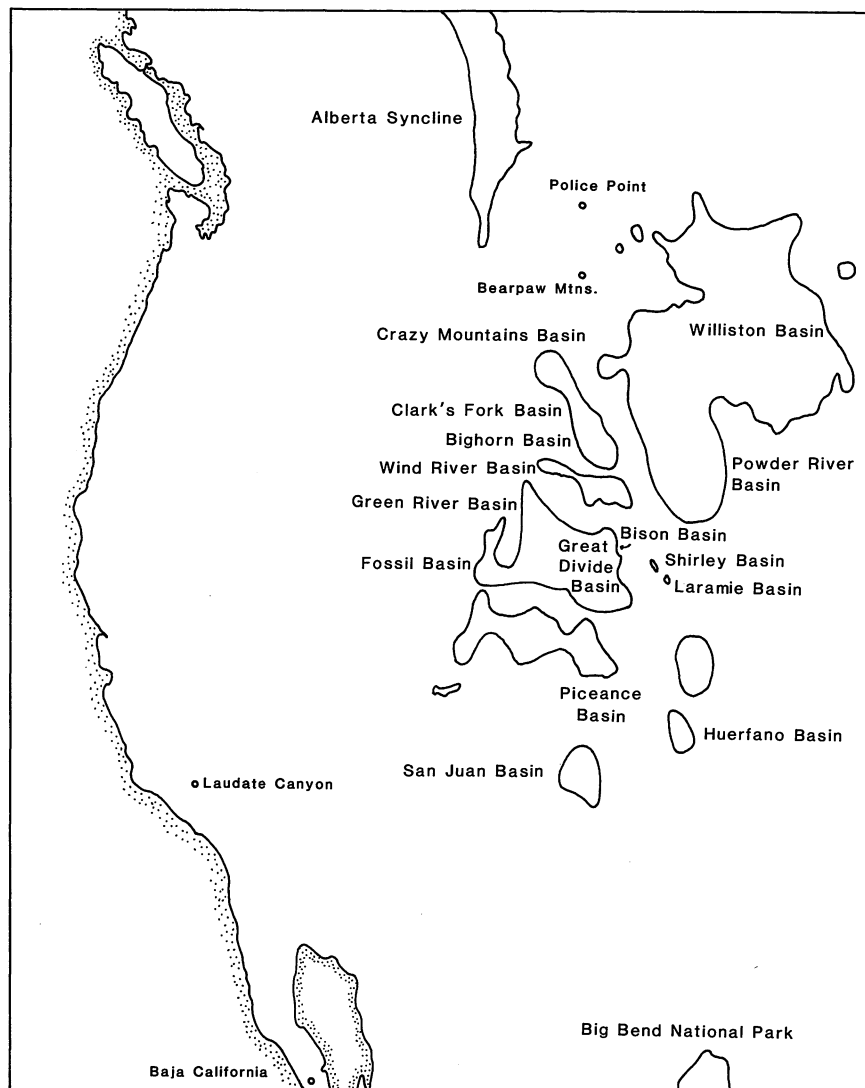
Figure 2. Areas yielding phenacodontids in western North America. Outlines indicate sedimentary basins; small circles indicate isolated localities.

Interval Zone for the time between the first appearance of *Bunophorus etsagicus* and the first appearance of *Heptodon*. This definition is tentative and can be improved when detailed stratigraphical work near the lower boundary of the zone in the Bighorn Basin is completed (Bown, pers. comm., 1988).

Schankler (1980) distinguished three zones in the late Wasatchian, the Lower, Middle, and Upper *Heptodon* Range Zone. The Lower and Middle *Heptodon* Range Zone are often combined into the Lysitean subage, and the Upper *Heptodon* Range Zone is known as the Lostcabinian subage (Gingerich, 1983). I will use the name *Heptodon/Lambdotherium* Range Zone to indicate the period between the

introduction of *Heptodon* and the introduction of *Lambdotherium*. For the period after the first appearance of *Lambdotherium*, I prefer the name used by Stucky (1984a, c): *Lambdotherium* Range Zone.

Phenacodontids are known from very few Bridgerian localities. Within the Bridgerian, I distinguish the earliest Bridgerian *Palaeosyops borealis* Assemblage Zone from all later Bridgerian. Stucky (1984a, c) discussed this zone in detail. I have not attempted to divide the later Bridgerian into biochrons.

In North America, phenacodontids range between 30° and 50° northern latitude and 100° and 125° western longitude. Within this range they are known from hundreds of

Table 1. North American land-mammal ages and biochrons as used here.

Bridgerian land-mammal age	Undifferentiated *Palaeosyops borealis* Assemblage-Zone
Wasatchian land-mammal age	*Lambdotherium* Range-Zone *Heptodon/Lambdotherium* Interval-Zone *Bunophorus etsagicus/Heptodon* Interval-Zone "Upper *Haplomylus-Ectocion* Zone" "Lower *Haplomylus-Ectocion* Zone" *Cantius torresi* Lineage-Zone
Clarkforkian land-mammal age	*Phenacodus-Ectocion* Acme-Zone *Plesiadapis cookei* Lineage-Zone *Plesiadapis gingerichi/P. cookei* Lineage-Zone
Tiffanian land-mammal age	*Plesiadapis simonsi/P. gingerichi* Lineage-Zone *Plesiadapis churchilli/P. simonsi* Lineage-Zone *Plesiadapis rex/P. churchilli* Lineage-Zone *Plesiadapis anceps/P. rex* Lineage-Zone *Plesiadapis praecursor/P. anceps* Lineage-Zone
Torrejonian land-mammal age	*Pantolambda/Plesiadapis praecursor* Interval-Zone *Tetraclaenodon/Pantolambda* Interval-Zone *Periptychus/Tetraclaenodon* Interval-Zone

localities. It is impractical to discuss all of these localities in detail, and instead I will discuss geographically clustered groups of localities, usually in the context of the sedimentary basin in which they occur. The order in which basins are discussed is more or less from north to south. Localities that are not in one of the larger basins of the Western Interior are discussed under heading of the geographically closest basin. For further information on many localities see Archibald et al. (1987) and Krishtalka et al. (1987).

Alberta Syncline

Just east of the Canadian Rocky Mountains is the Alberta Syncline, from which Puercan through late Tiffanian mammalian faunas have been described (Fox, 1988).

Phenacodontids have been reported from several localities in the foothills of the Canadian Rocky Mountains, but only a few specimens are published. L. S. Russell (1958) described Torrejonian *Tetraclaenodon* from his locality 2E near the city of Calgary (L. S. Russell, 1929, 1958; Fox, 1988). Phenacodontids from locality 1 near Cochrane were described by L. S. Russell (1929), and Gingerich (1982a) referred additional specimens from locality 2 (also referred to as II or 11; see Fox, 1988). These localities yield faunas from the *Plesiadapis praecursor* zone (Gingerich, 1982a). Simpson (1927) described phenacodontids from Erickson's Landing in the *Plesiadapis rex* zone (Gingerich, 1976a). L. S. Russell (1929) mentioned "phenacodontid?" material from a locality near the city of Red Deer, approximately 16 km west of Erickson's Landing. Undescribed phenacodontid specimens from the Alberta Syncline were listed

by Fox (1988) from the Tiffanian localities Hand Hills East, Joffre Bridge Roadcut, and Gao Mine.

Williston Basin

The Williston Basin is situated in North and South Dakota, Montana, and Saskatchewan. Faunas with phenacodontids range from Torrejonian through late Tiffanian.

Phenacodontids have been reported from a Torrejonian locality described by Lloyd and Harris (1915; see also Holtzman, 1978), who mention a single specimen identified by Gidley as "*Euprotogonia* sp." (now *Tetraclaenodon*). Three Tiffanian localities in North Dakota produced phenacodontids: Brisbane, Judson, and Riverdale (Holtzman, 1978). Archibald et al. (1987) list the *Plesiadapis rex* zone as the age for the former two localities, and the *Plesiadapis churchilli* zone as a tentative age for Riverdale, a conclusion that is corroborated by *Phenacodus* finds (see discussion of *P. magnus*).

A few phenacodontid localities are located in the part of the Williston Basin that extends into Montana. D. E. Russell (1967) listed *Tetraclaenodon* from the Circle fauna of northeastern Montana on the basis of an unpublished preliminary faunal list of R. E. Sloan. Wolberg (1979) published a more definitive faunal list with *Ectocion* as the only phenacodontid; the fauna is from the *Plesiadapis churchilli* zone. Krishtalka (1973) described a late Tiffanian fauna from the locality Police Point (also called UAR-1) near the Canadian northwest corner of the Williston Basin.

A single phenacodontid specimen comes from an undescribed Wasatchian locality in the Bearpaw Mountains, west of the Williston Basin (USNM field number H69–18A). The specimen was found by B. C. Hearn Jr.

Powder River Basin

Several Torrejonian, Tiffanian and Wasatchian mammal localities are known from the Powder River Basin of Montana and eastern Wyoming. Three sites are in the Medicine Rocks Area: the Torrejonian Medicine Rocks I (Rose, 1975; Sloan, 1987), and Tiffanian White Site and 7-Up Butte. Archibald et al. (1987) and Sloan (1987) consider the Tiffanian localities to be *Plesiadapis anceps* zone, apparently on the basis of Gingerich's (1976a:27) suggestion that *Plesiadapis* from these localities are probably *P. anceps*. The phenacodontids from these localities suggest that these localities may be younger (see discussion of *Ectocion cedrus* and *Phenacodus magnus*). Strait and Krause (abstract, 1988) state that new plesiadapid evidence is consistent with this. L. Robinson and Honey (1987) reported on the Tiffanian Newell's Nook locality.

Delson (1971) considered the Wasatchian biota of the Powder River Basin temporally and geographically restricted, and called them the Powder River Local Fauna. Delson suggested an earliest Wasatchian age for these fossils. Phenacodontids are known from eight localities de-

scribed by Delson (1971). Three more phenacodontid specimens from the same area and of approximately the same age are in the collections of the United States National Museum. More recent fieldwork by P. Robinson (University of Colorado) has yielded fossils from many levels spanning approximately 300 m of a published geological section in the Pumpkin Buttes area (Sharp et al., 1964). The locality that is lowest in this section (UCM locality 85279) has yielded one fossil in a prominent redbed near the base of the fossiliferous formation, a specimen of *Copecion davisi* (UCM 52888).

A specimen of *Phenacodus* was collected from higher strata on the north face of North Pumpkin Butte, and is reportedly *Lambdotherium* zone in age (Soister, 1968). This age determination was based on the supposed presence of *Lambdotherium*, although the original record for this specimen was "*Lambdotherium*?" (Sharp et al., 1964). The *Phenacodus* specimen is too fragmentary for identification but is probably *P. intermedius* or *P. trilobatus*.

Crazy Mountains Basin

The eastern Crazy Mountains Basin in south central Montana yields phenacodontids in late Torrejonian through middle Tiffanian faunas.

The stratigraphical relationships of many of the localities of the Crazy Mountains Basin were estimated by Simpson (1937b), but the outcrop pattern is not continuous (Krause and Gingerich, 1983; Butler et al., 1987). Torrejonian localities were referred to the *Pantolambda* zone by Archibald et al. (1987). The Tiffanian localities can be assigned to biochrons on the basis of data from Simpson's (1937b) stratigraphical section and the range zone system developed by Gingerich (1976a).

Phenacodontids from the Crazy Mountain Field were described by Douglass (1902, 1908), Simpson (1937b), West (1971), and Krause and Gingerich (1983). Rose (1981) published faunal lists for some of the quarry assemblages. Most workers have used Simpson's (1937b) locality numbers in referring to specific localities. Phenacodontids are known from the following Torrejonian localities: Silberling Quarry, Gidley Quarry, and localities 3, 6, 9, 25, 51, and possibly 5. Phenacodontids are also known from the following Tiffanian localities: Douglass Quarry, and localities 13, 27, 68, 70, 82, and possibly 11.

Simpson (1936) described an upper molar from Tiffanian Scarritt Quarry as "*Tetraclaenodon* sp." (p. 26), but he made no reference to this specimen when he published a comprehensive faunal list of the locality a year later (Simpson, 1937a). In the latter paper, the specimen (AMNH 33898) was probably included as "Phenacodont or Arctocyonid, Indet." (p. 11). AMNH 33898 is an arctocyonid in my opinion.

Only two phenacodontid specimens are known from the western Crazy Mountains Basin. An unnumbered and undescribed specimen of *Ectocion* at the University of Cincin-

nati is from a locality approximately 25 km west of the main fossiliferous area and was recovered on the "contact with Target Rock Laccolith." A cast of the specimen is at the American Museum (AMNH 96407). Roberts (1972) reported a specimen of *Tetraclaenodon* (USNM 22144), from the locality Willow Creek, nine miles north of Livingston.

Bighorn Basin

Thousands of predominantly Paleocene and early Eocene mammalian fossils have been collected in the Bighorn Basin of northwestern Wyoming and south central Montana. Some of the more recent faunal papers on the basin were published in a volume edited by Gingerich (1980), and in separate papers by Bown (1979), Rose (1981), and Gingerich (1989).

Stratigraphic relationships are known for many Bighorn Basin localities, and uninterrupted exposures in combination with simple structural relationships of the rocks in some parts of the basin have made it possible to tie many localities into measured sections, allowing analysis of large samples with tight stratigraphic control. A composite stratigraphic section for the Clarks Fork Basin was published by Gingerich (1976a, 1982b) and Rose (1981). Gingerich (1976b) published a section measured by G. Meyer and L. B. Radinsky in the Elk Creek area of the Bighorn Basin. Schankler (1980) published a section that he and S. L. Wing (Smithsonian Institution) measured in the Elk Creek area of the central Bighorn Basin. T. M. Bown (U.S. Geological Survey, Denver) measured a composite section extending mainly in the Elk Creek and Fifteenmile Creek areas of the central Bighorn Basin. The sections in the central Bighorn Basin were tied together and published with their vertebrate localities by Bown and Rose (1987). In this study I have employed the version of the central Bighorn Basin section published by Bown and Rose (1987), although recent research has shown that several meter levels above the *Bunophorus* zone need minor modifications (Bown, pers. comm., 1988).

The fossiliferous part of the Clarks Fork Basin section comprises one late Torrejonian sample (Rock Bench Quarry), few early and middle Tiffanian samples, and a continuous late Tiffanian through early Wasatchian sequence. The central Bighorn Basin section is fossiliferous from early through late Wasatchian. The two sections combined give a more or less continuous record of mammalian evolution from late Tiffanian through late Wasatchian. Old collections from the Bighorn Basin are substantial and contain many type specimens. This material remains important but lacks the detailed locality information that is now considered necessary. Because the material collected with tight stratigraphical control of the sections surpasses older collections in sample size and stratigraphic resolution, I have concentrated on the study of Bighorn Basin phenacodontids

(N = 4,500) from measured sections and a few isolated Torrejonian and Tiffanian assemblages.

Vertebrate fossils from the Bighorn Basin are preserved in rocks of different lithologies, indicating different depositional environments. Hickey (1980) interpreted Paleocene lithologies in the Clarks Fork Basin as indicative of paludal, lacustrine, and fluvial environments. Bartels (unpubl., 1987) considered Torrejonian and middle to late Tiffanian quarry assemblages to be deposited in poorly-drained systems, in contrast to the floodplain deposits that yield most younger Bighorn Basin fossils. Bown and Kraus (1981a, b, 1987) discussed differences in the sedimentary facies and taphonomy of the Wasatchian floodplain deposits. Different sedimentary facies may indicate habitat differences between represented taxa, and it can be expected that faunal composition in different sedimentary environments of similar age is different, as shown for a number of mammals by Winkler (1983), Gingerich (1989), and Bown and Beard (1990). Direct comparison of different habitats within one faunal zone is not always possible because fossils from a faunal zone are often restricted to one facies.

In the Bighorn Basin, middle and early late Tiffanian faunas are usually quarry assemblages and the sedimentary facies of these is indicative of a poorly-drained depositional environment. Floodplain deposits of the Bighorn Basin are the main fossiliferous units in latest Tiffanian and younger land-mammal ages. Animals from the floodplain deposits may have lived in habitats different from those in which animals found in quarries lived.

Phenacodontids from the Bighorn Basin are discussed in many papers: Granger (1915) and West (1976) used Bighorn Basin specimens in their reviews of the family Phenacodontidae. Simpson (1943) and Gingerich (1985) documented evolution of Bighorn Basin Ectocion, and Rose (1981) summarized the faunas from Torrejonian and Tiffanian quarry assemblages. Simpson (1937c) and Rose (1981) described Clarkforkian phenacodontids, and Bown (1979) described early Wasatchian taxa. Schankler (1981) discussed the pattern of phenacodontid evolution through the Wasatchian. Faunal papers on isolated localities are mentioned below.

Phenacodontids have been collected from hundreds of localities in the Bighorn Basin. Data on many of these localities have been published before (Bown, 1979; Gingerich et al., 1980; Schankler, 1980; Rose, 1981; Gingerich and Klitz, 1985; Bown and Rose, 1987; Gingerich, 1989). Here I will only discuss those localities that are of special importance for the present study. For convenience, and following many other workers, I will use the term "Clarks Fork Basin" for the northern extension of the Bighorn Basin. It is drained by the Clarks Fork River and extends north and west of Polecat Bench into Montana. I will refer to the rest of the Bighorn Basin as the central Bighorn Basin.

The extensive badlands called Cub Creek are near Belfry, Montana, and have yielded vertebrate fossils of late Torrejonian and early Tiffanian age. Published fossils from this area come from Torrejonian strata (Gingerich et al., 1980), but a few fossils have been recovered from levels in the Tiffanian Plesiadapis praecursor zone (Butler et al., 1987). A single Phenacodus bisonensis jaw (UM 80167) was recovered from an early Tiffanian locality (UM Eagle Quarry locality).

Late Torrejonian Rock Bench Quarry is on the southeastern edge of Polecat Bench. Rose (1981) published a faunal list for Rock Bench Quarry, and Bartels (unpubl., 1987) interpreted the depositional environment as an abandoned, locally reworked channel. Gingerich (1976a) based the terminal Torrejonian zone, which he designated "To₄," on the occurrence of Pronothodectes jepi at this locality. Archibald et al. (1987) include this zone in their Pantolambda/ Plesiadapis praecursor Range Zone (Butler et al., 1987). Torrejonian fossils were found in magnetic polarity chron 27N and Tiffanian fossils in chron 26R at Cub Creek. The magnetic polarity at Rock Bench Quarry is reversed, and Butler et al. (1987) proposed that Rock Bench Quarry is in chron 27R which is time equivalent to part of the San Juan Basin Torrejonian section. A second possible correlation of Rock Bench Quarry is with chron 26R, which would indicate that 26R is partly Torrejonian. Recognition of a separate Pronothodectes jepi zone is, in any case, based on faunal differences.

UM locality SC-337 and specimens in the YPM-PU collection from the "conglomerate above coal at Mantua mines" are only 0.5 km apart. These two localities north of Powell yield Ectocion collinus from the Plesiadapis anceps zone of Bighorn Basin. These localities are important because few early Tiffanian localities are known from the Bighorn Basin.

Rose (1981) published a faunal list for middle Tiffanian Cedar Point Quarry south of Lovell, Wyoming. This quarry has yielded the largest sample of phenacodontids from the Plesiadapis rex zone and the largest sample of phenacodontid jaw fragments from a single locality. Southwest of Cedar Point Quarry is Jepsen Quarry. The fossiliferous bed at Jepsen Quarry probably consists of clay-gall conglomerate, judging from sediment attached to fossils. Fossils are found in similar rock at Cedar Point, Divide, and Croc Tooth Quarries. Jepsen Quarry yields fossils from the Plesiadapis rex zone (Gingerich, 1976a).

Croc Tooth (or Witter) Quarry and Divide Quarry are south of Cedar Point Quarry and yield a fauna from the Plesiadapis churchilli zone. The largest phenacodontid sample from the Plesiadapis churchilli zone comes from these quarries.

Teams from Princeton University collected in August, 1951 at a locality "West-southwest of Sage Point," approximately a kilometer south of Mantua Quarry on Polecat Bench. Jaw fragments of two specimens of Ectocion and a large Phenacodus were found. These specimens are white, unlike the typical fossils from Clarks Fork Basin mudstone which are black. This suggests that the specimens may

have come from one of the conglomerates in this area. The mudstones underlying some of these conglomerates have yielded otherwise rare *Plesiadapis anceps* (UM locality SC-264). The phenacodontids at West-southwest of Sage Point suggest that it may yield fossils from the *Plesiadapis rex* zone.

A single specimen of *Ectocion cedrus* (UM 63277) was collected at Long Draw Quarry. This quarry is important because it is the type locality of *P. churchilli* (Gingerich, 1976a). Long Draw Quarry is north of Polecat Bench.

The Seaboard Well locality is west of the Elk Creek Anticline, and north of the main fossiliferous areas in the Clarks Fork Basin (Gingerich et al., 1980). Archibald et al. (1987) list the age of this locality as middle Tiffanian, but evidence from phenacodontids presented below (see discussion of *E. cedrus* and *P. magnus*) is inconsistent with this, and suggest that it dates from the *Plesiadapis churchilli* zone.

The Bear Creek locality is on the northwestern edge of the Clarks Fork Basin, west of Cub Creek. Simpson (1928, 1929a, c) originally described the fauna, and Rose (1981) updated the faunal list. Simpson (1929c) described one of two phenacodontid specimens known from Bear Creek. The aberrant composition of the Bear Creek fauna (Rose, 1981) and its occurrence with coal, suggested that the sediment from the quarry was deposited in a paludal environment (Van Valen and Sloan, 1966).

Krause Quarry (within UM locality SC-195) was discovered by D. W. Krause and P. D. Gingerich in 1978. The matrix of the quarry consists of grayish green sand- and siltstone, and it yields a middle Clarkforkian faunal assemblage. The locality is unusual in yielding an abundance of postcranials. *Ectocion* is the most common taxon at this locality.

UM locality SC-67 was discussed in detail by Gingerich (1989). It is one of a few localities that yield fossils from the *Cantius torresi* zone.

Few faunal papers have been published on the hundreds of Wasatchian localities in the Clarks Fork and central Bighorn Basin. Many of these localities are tied into the stratigraphic sections described before, and are thus of particular importance to the study of faunal evolution.

Torres (1985) gave a summary of stratigraphy and fossil vertebrates found near Jim Creek on the North Fork of the Shoshone River. These localities are approximately 30 km west of Cody. Torres (1985) listed one of several *Phenacodus* specimens from the *Lambdotherium* zone.

Eaton (1982) reported *Phenacodus* from a locality on Carter Mountain, on the west edge of the Bighorn Basin. He considered the locality (UW locality 78001) equivalent to Bridger C in age.

A specimen of *Phenacodus* (UW 14552) was found in badlands approximately 30 km west of Meeteetse (UW locality 79011). These outcrops are not in the same depositionary basin as the early Tertiary deposits of the central Bighorn Basin.

Wind River Basin

The Wind River Basin of central Wyoming is best known for its late Wasatchian faunas, but early Bridgerian as well as Tiffanian and Clarkforkian assemblages with phenacodontids have been reported.

Phenacodontids are known from two late Tiffanian localities in the north central Wind River Basin. Krishtalka et al. (1975) described phenacodontids from Malcolm's locality (also called the Badwater locality) in the *Plesiadapis churchilli* zone (Gingerich, 1976a). A specimen (CM 16200) referred to *Phenacodus* sp. by Krishtalka et al. (1975) is probably an arctocyonid. West of Malcolm's locality is an undescribed locality of the University of Colorado: Richard's locality (UCM locality 79038). Phenacodontids from this locality indicate that it is not early Tiffanian, but do not constrain the age beyond this. A single specimen of *Ectocion* from Richard's locality (UCM 42006) is too fragmentary for further identification.

Tiffanian, Clarkforkian, and Wasatchian faunas have been recovered in the area of Shotgun Butte in the northwestern part of the Wind River Basin (Keefer and Troyer, 1956; Keefer, 1965; Gunnell, 1989). Phenacodontids are known from a locality called Keefer Hill by MacIntyre (1966; "Twin Buttes" of some, but not all authors). This site yields fossils from the *Plesiadapis praecursor* zone (Archibald et al., 1987; Gunnell, 1989), and is close to a middle Clarkforkian locality called "Shotgun Butte proper" by Gazin (1971) and "West of Shotgun Butte" by Archibald et al. (1987). The latter is presumably the same as locality 20 of Keefer and Troyer (1956). Phenacodontids from the *Lambdotherium* zone near Shotgun Butte were reported by Keefer and Troyer (1956, 1964). Several phenacodontids were recovered at locality 21 of Keefer and Troyer (1956). Two *Ectocion* specimens (USNM 187502 and 187506) from this locality are larger than average *Ectocion osbornianus*, although the suggestion on the label that they might be referable to *Ectocion superstes* seems unlikely.

Underlying the very fossiliferous late Wasatchian and early Bridgerian Wind River Formation is the Indian Meadows Formation, from which few fossils have been described. A small collection from this formation is at the U. S. National Museum, and was reported by Keefer and Troyer (1964) and Keefer (1965). Remains of three phenacodontid taxa were collected at locality 13E of Keefer, and suggest that this locality may yield a fauna from the Upper *Haplomylus-Ectocion* zone. Winterfeld and Conard (1983) published a faunal list for the Indian Meadows fauna from localities near Dubois. These faunas may be early to middle Wasatchian in age.

Phenacodontids occur in the *Heptodon, Lambdotherium*, and *Palaeosyops* zones of the Wind River Formation of the Wind River Basin. Most of the specimens are from the northeastern part of the basin. Descriptions of localities can be found in Keefer (1965), Black and Dawson (1966), Guthrie (1967, 1971), and Stucky (1984a, b). Faunas with

phenacodontids were described by Kelley and Wood (1954), Guthrie (1967, 1971), Stucky and Krishtalka (1982), and Stucky (1984a, c). Guthrie (1967) noticed that Kelley and Wood (1954) mistook a P_3 of *Hyracotherium* for a P_4 of *Phenacodus brachypternus* (ACM 10200, now referred to the genus *Copecion*). Recent collecting efforts by teams from Carnegie Museum have resulted in the recovery of two new skulls and associated skeletons of *Phenacodus vortmani* and additional specimens of *Ectocion superstes*. West and Atkins (1970) described a specimen of *Phenacodus* from the Wind River Basin that they thought might be of Bridgerian age (CM 12476). Bown (1982) also reported Bridgerian *Phenacodus* from the Wind River Basin.

McKenna (1980) reported phenacodontids from a number of localities in the Togwotee Pass area: middle Tiffanian Love Quarry, latest Tiffanian or early Clarkforkian Low locality, and the middle Clarkforkian Red Creek localities. A single *Phenacodus* specimen (AMNH 86728) from the Low locality is too fragmentary for identification. Fieldwork since 1980 by M. C. McKenna has yielded phenacodontids from a number of additional Clarkforkian localities. A few Togwotee Pass phenacodontids are in the USNM collection, these are mainly from a locality near the Du Noir River. I have not studied the specimens identified as *Ectocion parvus* by McKenna (1980).

Green River Basin

Tiffanian through Bridgerian phenacodontids have been reported from the Green River Basin in southwestern Wyoming. Dorr (1958, 1978) described Tiffanian through Wasatchian faunas from the Hoback Basin at the northern edge of the Green River Basin. Phenacodontids are known from the Battle Mountain Local Fauna (UM-Sub-Wy localities 21 and 22), which yields fossils from the *Plesiadapis rex* zone (Gingerich, 1976a). A specimen of *Phenacodus* was the only fossil found at each of UM-Sub-Wy localities 10 and 20. Both these localities are probably early Clarkforkian in age (Dorr, 1978). I did not see an uncatalogued phenacodontid M^3 from UM-Sub-Wy locality 7 that was reported by Dorr (1958).

Dorr and Gingerich (1980) also described the fauna from a locality that Gazin (1956c) discovered: Chappo Type locality near LaBarge. This locality yields fossils from the *Plesiadapis rex* zone. Dorr and Gingerich (1980) reported phenacodontid remains from a third locality "along the crest of Hogsback Ridge between LaBarge Creek and Chappo Gulch" (p. 110). As indicated by these authors, the phenacodontid remains from this site are too fragmentary for exact identification.

Phenacodontids have also been found at a few Tiffanian and Clarkforkian localities west of LaBarge in the Green River Basin. Gazin (1956c) described the fauna from the locality Buckman Hollow, and Dorr and Gingerich (1980) reviewed the fauna and considered the age of Buckman

Hollow to be *Plesiadapis cookei* zone. Two fossiliferous areas occur in the Buckman Hollow area, in respectively Section 1 and 12 of T26N, R114W. Gingerich (1976a) considered the outcrops in Section 1 (his Chappo-1, UM localities Buckman Hollow 5 and 6) tentatively early Clarkforkian and the larger section present in Section 12 (his Chappo-12, UM localities Buckman Hollow 1 through 4) middle Clarkforkian. The middle Clarkforkian age is based on the presence of *Plesiadapis cookei*, but specimens of this taxon in the UM collection are only known from the upper parts of the stratigraphic section of Section 12 (UM localities 3 and 4). One phenacodontid specimen from Buckman Hollow is relatively complete and can be referred unambiguously to Tiffanian *E. mediotuber*. This specimen (USNM 20736) was found in the lower part of the stratigraphic section, "NW $1/4$, NE$1/4$, Sec. 12," (UM locality 1, 2, or 3). Rose (1981) reported additional Tiffanian taxa from Buckman Hollow. Other specimens of *Ectocion* and a few *Phenacodus* cannot be identified with certainty, and I will follow Archibald et al. (1987) and consider all these specimens Clarkforkian.

West (1973) described a fauna from the *Lambdotherium* zone of the New Fork-Big Sandy area of the northeastern Green River Basin. Two fragmentary specimens that West described as phenacodontids are probable large dichobunids (FMNH PM 15509 and 15575). Phenacodontids are known from four localities in this area. I have not seen two specimens from the locality Steele Butte Breaks (FMNH PM 15510 and 15605).

A Bridgerian phenacodontid is known from *Hyopsodus* Hill in the Tabernacle Butte area. West and Atkins (1970) described and discussed this specimen and its occurrence in Bridgerian rocks.

Fossil Basin

Gazin (1952, 1962) reviewed the Wasatchian fossil collections from the Fossil Basin, west of the Green River Basin. Gazin (1952, 1956b) reported phenacodontids from the locality Twin Creek: "3 miles east of Fossil Station" (Gazin, 1952:6). The locality is *Plesiadapis rex* zone in age (Gingerich, 1976a). A single specimen of *Phenacodus* (USNM 22433) was found in the "Low exposures about 2 mi SW of Elk Mtn." according to its label. The fauna may be Lower or Upper *Haplomylus-Ectocion* Zone in age (Gazin, 1962).

The holotype of *Phenacodus primaevus* Cope, 1873 (AMNH 4408) was found 11 miles southeast of Evanston on Bear River according to Gazin (1952), at a locality that is sometimes referred to as Knight Station (Gazin, 1962). This area has produced *Heptodon* (Granger, 1914), suggesting that the fauna may be from the *Heptodon* zone.

Bison Basin

Early to late Tiffanian vertebrates are known from the Bison Basin, south of the Granite Mountains in central

Wyoming. All fossil localities are concentrated in Sections 28 and 29 of T27N, R95W. Gazin's (1956a) descriptions are based on fossils from four localities, but additional localities have been found subsequently. Phenacodontids are known from two localities in the *Plesiadapis anceps* zone: the Saddle locality of Gazin, and the High Saddle locality. Gazin (1956a:3) refers to the latter locality as being 50 feet above the Saddle. Phenacodontid localities in the *Plesiadapis rex* zone are Gazin's Ledge locality (sometimes, but not always, synonymous with "S-Rim") and West End locality, and in the *P. simonsi* zone Bell's locality (also called *Titanoides* locality). The fauna from UCMP locality Cairn Hill is probably from the *Plesiadapis anceps* zone. The UCM Mistake locality and the UCMP locality Bison Basin 1 yield fossils from the *Plesiadapis rex* zone, and the same is probably true for the USNM Brown Saddle locality.

Great Divide, Washakie, and Sand Wash Basins

Phenacodontids in faunas from Torrejonian through Wasatchian age were found in the Great Divide, Washakie, and Sand Wash Basins of southcentral Wyoming and northern Colorado.

Rigby (1980) described the Torrejonian fauna from Swain Quarry in the eastern Washakie Basin. This fauna was tentatively referred to the *Pantolambda* zone by Archibald et al. (1987). Winterfeld (1982) described Torrejonian and Tiffanian phenacodontids from localities in a stratigraphic section east of the Rock Springs Uplift. A Torrejonian specimen was discovered (UW 13236) at a level from which also *Pronothodectes* sp. cf. *P. jepi* is reported. Phenacodontids were also found at four localities in the *Plesiadapis churchilli* zone and three localities in the *Plesiadapis simonsi* zone.

Winterfeld (1982) listed *Ectocion* from a supposedly Torrejonian locality (UW locality V-77014). Localities between the 61 and 87 m level were considered Torrejonian on the basis of the presence of *Acmeodon, Anisonchus, Aphronorus, Gelastops, Paromomys, Pronothodectes,* and *Tetraclaenodon* (Winterfeld, 1982:77). Of these only *Acmeodon, Anisonchus, Aphronorus,* and *Paromomys* were found as high in the section as the supposed Torrejonian *Ectocion* specimens, and these taxa have been reported from Tiffanian as well as Torrejonian land-mammal ages (Archibald et al., 1987). *Ectocion* is not known from Torrejonian deposits of other areas and I therefore assume that this specimen is from an early Tiffanian fauna. Rose (1981) published a faunal list for UCMP Big Multi Quarry (locality V-76134). This locality has yielded several phenacodontids from the *Plesiadapis cookei* zone.

Gazin (1962) described a phenacodontid specimen from the Wasatchian Red Desert locality in the western Great Divide Basin (USNM 205738). Gazin (1962) also described an undiagnostic *Phenacodus* specimen from southwest of Bitter Creek (USNM 22668). The presence of *Hap-*

lomylus at both localities suggests that they may yield fossils from the Lower or Upper *Haplomylus-Ectocion* zones. Teams from the University of California at Berkeley have discovered several undescribed localities from the Bitter Creek area. A specimen of *Ectocion osbornianus* was recovered at the Clarkforkian locality "Bitter Creek Road 1."

McKenna (1960) described the Four Mile fauna from the Sand Wash Basin in northwestern Colorado. The fauna is known from more than 20 localities and is considered early Wasatchian in age. Evidence from the Four Mile phenacodontids is partly consistent with the interpretation of this fauna as Lower *Haplomylus-Ectocion* zone, although the abundance of *P. trilobatus* is greater than in the Lower *Haplomylus-Ectocion* zone of the Bighorn Basin. It is possible that a number of Four Mile localities are actually Upper *Haplomylus-Ectocion* zone. *Phenacodus trilobatus* and *P. vortmani* co-occur at a single Four Mile locality (Despair Quarry). The combination of these taxa suggests Upper *Haplomylus-Ectocion* zone for Bighorn Basin localities, although this is possibly in part due to factors other than time (see Chapter IV). The Four Mile Fauna may actually straddle the boundary between Lower and Upper *Haplomylus-Ectocion* zone, which is consistent with interpretations of Four Mile microsyopids by Gunnell (1985 and 1989).

Laramie and Shirley Basins

Princhinello (1971) and Davidson (1987) described Wasatchian faunas with phenacodontids from the Cooper Creek Area of the Laramie Basin in southeast Wyoming. The age of the fauna may be near the boundary of Lower and Upper *Haplomylus-Ectocion* zone (Davidson, 1987).

Harshman (1972) reported a specimen of *Phenacodus* cf. *primaevus* from a locality in the Wind River Formation of the Shirley Basin of southeastern Wyoming. *Hyrachyus* was reported from the same locality, suggesting that the fauna may be younger than *Lambdotherium* zone (Stucky, 1984c). University of Wyoming's "Pat Holiday's Fence locality" in the Wind River Formation yielded *Phenacodus vortmani* (UW 2161). No age estimate is available for this locality but it is plausible that the two localities with phenacodontids are both *Lambdotherium* zone or younger.

Piceance Basin

The Piceance Basin of northwestern Colorado yields faunas of Clarkforkian through late Wasatchian age and possibly also late Tiffanian age. Kihm's comprehensive work (unpubl., 1984) on all Piceance Basin faunas remains unfortunately unpublished. A now outdated Wasatchian faunal list was published by Van Houten (1945), and a tentative faunal list for Paleocene faunas based on Kihm's work was published by Rose (1981). Archibald et al. (1987) indicated that the age of the older faunas is possibly *Plesiadapis gingerichi* zone, but some Tiffanian specimens

may be present (Rose, 1981). *Phenacodus* and *Ectocion* from these presumed Clarkforkian localities of the Piceance Basin do not preserve teeth that identify them unambiguously as Tiffanian or Clarkforkian taxa: among seven specimens of *Ectocion* no complete posterior premolars are preserved (see discussion of *E. mediotuber*). Among 25 specimens of large *Phenacodus* a single P^4 is preserved. This specimen has a length/width ratio intermediate between the modes for *P. grangeri* and *P. intermedius* (see discussion of *P. intermedius*). I follow Kihm (unpubl., 1984) in considering these faunas Clarkforkian until new evidence becomes available.

Huerfano Basin

The Huerfano Basin of southcentral Colorado yields faunas from late Wasatchian and early Bridgerian age. P. Robinson (1966) described the fauna in detail and Stucky (1984c) outlined a refined faunal zonation for the basin. Phenacodontids are known from Robinson's (1966) localities 6 and 9. These localities yield faunas from respectively the *Heptodon* and *Lambdotherium* zones (Stucky, 1984c). A specimen questionably referred to *P. vortmani* by Robinson (1966; AMNH 17548) is probably a large arctocyonid.

San Juan Basin

The San Juan Basin of southwestern Colorado and northwestern New Mexico yields Torrejonian, Tiffanian, and Wasatchian faunas with phenacodontids. Matthew (1897, 1937) described the Torrejonian faunas in detail, and recently Taylor (unpubl., 1984) reviewed these faunas. The phenacodontid *Tetraclaenodon* ranges through two Torrejonian biochrons of the San Juan Basin: the *Tetraclaenodon* and *Pantolambda* zones (Archibald et al., 1987). Large collections of *Tetraclaenodon* have been accumulated in the past, but precise locality data for many of these specimens is limited. Collections of Torrejonian vertebrates with adequate stratigraphic control are available now (e. g., R. W. Wilson; 1956 and Taylor, unpubl., 1984). Taylor (unpubl., 1984) analyzed a large collection of *Tetraclaenodon* in stratigraphical context (see also Lindsay et al., 1981) and made inferences concerning the evolution of *Tetraclaenodon* in the San Juan Basin. Taylor's material is unavailable for study.

The type Tiffanian "Tiffany Fauna" is found at a number of localities in the northern part of the San Juan Basin. Simpson (1935b) published a faunal list and Simpson (1935c) described the Tiffany phenacodontids. The best known locality among the Tiffany sites is "Mason Pocket," a mudstone lense due north of the town of Tiffany. This locality is near the base of the exposed section and has yielded *Nannodectes gidleyi*, a taxon restricted to the *Plesiadapis churchilli* zone (Gingerich, 1976a). Two specimens of *Phenacodus* are from Mason Pocket according to their labels (AMNH 17191 and 56286). The former of these is the holotype of *Phenacodus matthewi*, and there is little

doubt that this specimen is in fact not from Mason Pocket (see discussion of *P. matthewi*). AMNH 56286 is an upper molar collected in 1951 by G. O. Whitaker. Whitaker's field notes and G. G. Simpson's unpublished notes on the collection leave some doubt whether the locality information on the label is correct. The specimen might be identified with field number Colo-11B in Whitaker's notes, indicating that it came from Mason Pocket, but it is more likely that its fieldnumber is Colo-9, and that it was collected 60' above Mason Pocket.

Concerning a third specimen Simpson's notes state: "Not really identifiable at present, but I suspect this is the same species as" *Phenacodus matthewi* (Simpson did not use the latter name, but referred to that taxon by description). This specimen was recovered at Mason Pocket, but it is unclear to which specimen the remark refers. Many localities in the vicinity of Mason Pocket yield late Tiffanian or even Clarkforkian fossils.

Reeside (1924) mentioned phenacodontids from two other Tiffanian localities. One of these is commonly referred to as "5.5 miles east of Bayfield." According to Reeside (1924), this locality has yielded only three fossils among which *"Tetraclaenodon* or *Phenacodus"* (p. 47), apparently USNM 10649. Another locality described by Reeside (1924:47) is "one mile west of Carracas station, Colo., on the Denver & Rio Grande Western Railroad, at the edge of the hills north of the railroad; horizon in the lower 100 feet of the "Tiffany Beds" (1924:47). I have studied only four of the seven phenacodontid specimens from this locality listed by Reeside (1924) and one additional specimen (UM 71351; from 5.5 miles east of Bayfield).

The age of at least one of the two localities of Reeside (1924) is unclear. Gidley (1923) states in a figure caption that USNM 10639, a left upper incisor described as *"Nothodectes* cf. *gidleyi* Matthew or new species" (p. 38) was found "5.5 miles east of Bayfield," but Reeside, who collected the specimen, does not list it as one of the finds from that locality, but cites: "Nothodectes cf. *N. gidleyi* or new species. A left upper incisor . . . " from "one mile west of Carracas Station" (p. 47). Gingerich (1975) made this specimen the holotype of *Chiromyoides potior* and stated that the age of the type locality was *P. simonsi* zone. The type locality is either "5.5 miles east of Bayfield," as claimed by its label and Gidley or "one mile west of Carracas Station," as claimed by Reeside's fieldnotes.

Wasatchian faunas with phenacodontids are also known from the San Jose Formation in the southeastern part of the San Juan Basin. A review of these faunas with faunal lists was published by Lucas et al. (1981). These faunas may be from the *Heptodon* zone.

Big Bend National Park

J. A. Wilson (1967) and Schiebout (1974) described Tiffanian through Wasatchian faunas with phenacodontids

from Big Bend National Park in southern Texas. Fossil localities were tied to a stratigraphical section by Schiebout (1974) and correlated magnetostratigraphically by Rapp et al. (1983) and Schiebout et al. (1987).

Phenacodontids from Big Bend have been recovered from five levels in Schiebout's section. The oldest locality that yields phenacodontids is at 23 m. This level is considered to be on the Torrejonian-Tiffanian boundary by Rapp et al. (1983), and to be in the *Plesiadapis praecursor* zone by Archibald et al. (1987). The Torrejonian age cited by Rapp et al. (1983) is based on the recovery of a specimen of Torrejonian *Promioclaenus acolytus* and an isolated lower molar of *Palaeotomus senior* from the same locality as the phenacodontids (Schiebout, 1974, and pers. comm., 1988). Phenacodontids from this locality are more consistent with *Plesiadapis rex* zone age for this locality (see discussion of *Phenacodus grangeri*). This interpretation is also consistent with paleomagnetic data published by Rapp et al. (1983).

Phenacodontids are also known from the Eastern Tornillo Flats (locality T2 of J. A. Wilson, 1967). Archibald et al. (1987) state that this locality is possibly from the *Plesiadapis rex* zone. Higher in the section are localities at the Western Tornillo Flats (partly locality T1 of J. A. Wilson, 1967) and Ray's Bone Bed, which are both *Plesiadapis rex* zone (Gingerich, 1976a). The Oil House locality yields Wasatchian phenacodontids (J. A. Wilson, 1967).

Laudate Canyon

A single specimen of *Tetraclaenodon* (UCMP 69122) was collected in the Goler Formation of Laudate Canyon, Kern County, California. The specimen occurred as isolated float, and is the youngest Torrejonian fossil from the area. The specimen was described by West (1970), and McKenna et al. (1987) reported on the paleontology of the Goler Formation.

Baja California

Novacek et al. (1987) listed *Phenacodus vortmani* and a new species of *Ectocion* from Lomas las Tetas de Cabra in Baja California. I have not studied these specimens. According to Flynn et al. (1989) the assemblage is Wasatchian in age.

EUROPEAN BIOCHRONOLOGY AND LOCALITIES

European phenacodontids are known from the Eocene of Britain, Belgium, France and Spain, and from Dormaalian, Grauvesian, and Robiacian land-mammal ages (respectively equivalent to Sparnacian, Cuisian, and Lutetian).

Rich (1971) discussed many European phenacodontids, and a listing of the associated fauna and stratigraphical

relation of the localities was published by Russell (1982), Russell et al., (1982), Savage and Russell (1983), and Godinot (1988). Franzen and Haubold (1986b) described middle Eocene *Hallensia* as a phenacodontid, but the recovery of more material indicates that it is in fact a perissodactyl (Franzen, pers. comm., 1988). Antunes and Russell (1981) reported a phenacodontid from the Portuguese locality Silveirinha. The specimen in question is an isolated M_3 with a high trigonid and a conical entoconid (D. E. Russell, pers. comm., 1988). This tooth is unlike phenacodontids in these characters.

Paris Basin

Phenacodontids are known from the localities Dormaal, Mutigny, Avenay, Pourcy, Condé-en-Brie, and Grauves in the Paris Basin (Lemoine, 1891; Teilhard de Chardin, 1922, 1927; Louis, 1966; Rich, 1971).

The oldest localities with European phenacodontids are Dormaal and Pourcy, followed by Avenay, Mutigny, and Condé-en-Brie (Russell et al., 1982; Godinot, 1988). Lemoine (1891) and Teilhard de Chardin (1922) described a few phenacodontid specimens from one or more localities near the city of Epernay. The exact provenance of these specimens is unknown (Russell, pers. comm., 1988), but they are equivalent in age to Avenay. A P^4 identified as *Phenacodus* by Teilhard de Chardin (1922) is in fact a perissodactyl (MNHN AL 5178). The localities in France and Belgium yield fossils traditionally assigned to the earliest Eocene Sparnacian (Savage and Russell, 1983), and referable to the Dormaalian land-mammal age (Russell, pers. comm., 1988), or MP 7–9 of Godinot (1988). Fossils from the locality Grauves are referred to the subsequent Grauvesian land-mammal age (Franzen and Haubold, 1986a; D. E. Russell, pers. comm., 1988). No phenacodontids are known from the Geiseltalian land-mammal age which follows the Grauvesian.

London Basin

Small tooth fragments of *Phenacodus* are known from Abbey Wood in the London Basin. This locality is Dormaalian in age (Collinson and Hooker, 1987; Hooker, pers. comm., 1988).

Tremp Basin

Spanish phenacodontids come from Sierra de Montllobar and Barranc de Forals (Crusafont Pairo and Villalta Comella, 1955; Crusafont Pairo, 1956a, b; Russell et al., 1982). Crusafont Pairo and Villalta Comella (1954) described *Almogaver condali* (= *Phenacodus condali*) as a new Eocene primate. Crusafont Pairo (1956a, b) described the holotype and only specimen of *P. villaltae* and a P_4 referred to *P. cf. teilhardi*. I have not seen either of these latter specimens, but Crusafont Pairo's (1956b) figure 1 leaves some doubt as to whether these are really *Phena-*

codus. Phenacodontids from Sierra de Montllobar can be referred to the Robiacian land-mammal age, equivalent to Lutetian. Ginsburg and Mennessier (1973) described two phalanges from the Eocene of Spain (near Salernes) that pertain to an unidentified phenacodontid.

Isabena Basin

Undescribed phenacodontids from Spain are known from the localities El Pueyo and possibly Castigaleu in the Isabena Basin according to D. E. Russell (1982 and pers. comm., 1988). El Pueyo is Grauvesian in age.

III
SYSTEMATIC PALEONTOLOGY

Order CONDYLARTHRA Cope, 1881

Cope (1881a) originally diagnosed Condylarthra as a suborder of the order Perissodactyla, and chose two diagnostic characters: the astragalar head is convex and articulates with the navicular only, and the femur has a third trochanter. The shape of the astragalus in condylarths is primitive in many respects, and distinguishes this order from some of the orders derived from condylarths. The astragalar head of artiodactyls bears a trochlea (Schaeffer, 1947), and it is saddle-shaped in perissodactyls and hyracoids (Fischer, 1986). Proboscidea have a medial tubercle on the astragalar trochlea (Tassy and Shoshani, 1988). However, the head of the astragalus does not distinguish condylarths from many other placentals. The presence of a third trochanter is also problematical. It is a primitive feature that is retained in many other orders, such as perissodactyls and early artiodactyls (Rose, 1981).

Cope (1881a) designated Phenacodontidae as type- and only family of Condylarthra. Cope (1885) raised Condylarthra to the level of an order, and included many early Paleogene moderate to large placentals with generalized dentitions and postcranials. Condylarthra was always considered a para- or polyphyletic group (e. g., Simpson, 1945; Van Valen, 1978). The term was considered useful as a heuristic device in the absence of a stable phylogeny.

McKenna (1975) returned to a more restricted idea of Condylarthra in order to resolve some of the vagueness surrounding the concept. Prothero et al. (1988) proposed to abandon the term altogether but did not propose a new ordinal classification for the included taxa. I will here take a conservative position until more evidence for affinities among early ungulate groups accumulates: following Cope (1882a) and most later authors, I include the family Phenacodontidae in the order Condylarthra.

Prothero et al. (1988) delimited condylarths and the orders derived from them as follows: superior ramus of stapedial artery shifted to petrosal or lost; mastoid foramen lost; bulla (if present) composed of ectotympanic; relatively bunodont teeth with low cusp relief; lower molar trigonids shortened anteroposteriorly; large, posteriorly projecting hypoconulid on M_3; astragalus with short robust head. Condylarths can be characterized as those that have these characters, but lack the specializations of the orders derived from them.

Family PHENACODONTIDAE, Cope, 1881

Type genus.—*Phenacodus* Cope, 1873a.

Referred genera.—*Ectocion* Cope, 1882i; *Tetraclaenodon* Scott, 1893; *Copecion* Gingerich, 1989.

Diagnosis.—Bunodont to bunolophodont condylarths. P_4 with talonid basin and subequal protoconid and metaconid. Paraconid of lower molars absent or small. P^3 with small protocone, P^4 with paracone, metacone, and protocone. M^{1-2} with hypocone and often with mesostyle. Dental formula: 3.1.4.3 / 3.1.4.3. Humerus with weak deltopectoral crest and supracondylar foramen. Ulna strong with anterior process distally. Five digits in hand and foot. Femur with third trochanter. Fibula complete. Astragalus with convex head.

Arctocyonidae differ from Phenacodontidae in having less inflated molar cusps and unmolarized premolars. Hyopsodontidae differ from Phenacodontidae in having higher trigonids, no metacone on P^4, and smaller hypocones. Meniscotheriidae differ from Phenacodontidae in having more lophodont, hypsodont molars. Didolodontids differ from phenacodontids in the absence of a talonid basin of P_4, and the more molarized P^3. Periptychidae differ from Phenacodontidae in the labial position of the protocone and inflated posterior premolars (Archibald et al., 1983). Mesonychidae differ from phenacodontids in the reduction of the trigon, trigonid, and talonid basins, and the inflation of individual cusps.

Description.—Molars bunodont (*Tetraclaenodon, Phenacodus, Copecion*) to somewhat lophodont (*Ectocion*). Lower incisors spatulate, lower canine higher than other lower teeth, rounded in cross section, and enamel surface with shallow longitudinal furrows. P_1 single rooted, with pointed crown and strong posterior cingulum. P_2 double rooted, with protoconid, weak talonid, and small hypoconid. P_3 with protoconid, metaconid weak or absent, paraconid small and on cingulum if present, talonid with hypoconid. P_4 with strong protoconid and metaconid, trigonid basin present, paraconid present or absent, hypoconid strong, entoconid present or absent. Lower molars with low trigonid and shallow trigonid basin, paracristid and metacristid present, protoconid and metaconid of similar size, paraconid usually absent. Metastylid usually present posterior to metaconid, protostylid sometimes present posterior to protoconid. Lower molar talonid with entoconid, hypoconid, and hypoconulid. Hypoconulid of M_3 inflated, forming a third lobe.

Upper incisors pointed (anterior incisors wear flat), and spaced in the premaxilla. Upper canine rounded in cross section, higher than other upper teeth, and enamel surface with shallow longitudinal furrows. P^1 single or double rooted. P^2 with two roots, wider posteriorly than anteriorly, protocone absent, postparacrista sometimes with one or more cusps (metacone). P^3 with strong paracone and weak meta- and protocone, paraconule sometimes present. P^4 with similar sized paracone, metacone, and protocone; paraconule and parastyle usually present and metaconule sometimes present; mesostyle and hypocone always absent. M^{1-2} with strong hypocone, parastyle, and mesostyle, variable conules, labial cristae W-shaped, sometimes weak ectoloph, protoloph and metaloph never present. M^3 similar to M^{1-2}, but posterior half reduced to variable degrees, metacone, hypocone, and/or mesostyle may be absent.

Discussion.—Cope (1881a) created the family Phenacodontidae for a number of perissodactyls including *Phenacodus* and "very probably" *Protogonia* (here referred to as *Tetraclaenodon*). Cope (1882c) considered *Ectocion* a perissodactyl as well, but suggested chalicothere affinities, while keeping the condylarth option open. Cope held this opinion until much later, although he also suggested a relationship between *Ectocion* and primitive tapiroids (1887).

Granger (1915) included *Ectocion* in Phenacodontidae. He was followed in this by all subsequent authors. *Tetraclaenodon, Phenacodus,* and *Ectocion* have since then formed the core of phenacodontids. North American *Desmatoclaenus* was included in the family by Simpson (1945) and West (1976), and European *Tricuspiodon* by Rigby (1980), but these inclusions did not meet general acceptance (Cifelli, 1983), and are not followed here. Patterson and West (1973) created the new North American genus *Prosthecion,* which I consider synonymous with *Ectocion,* and Gingerich (1989) moved "*Phenacodus*" *brachypternus* to the new genus *Copecion.* Van Valen (1978) and Prothero et al. (1988) published a detailed phylogenetic hypothesis for phenacodontids and related forms at the generic level. I consider European *Almogaver* a synonym of *Phenacodus* (see below). Other genera sometimes referred to Phenacodontidae were discussed in Chapter II.

The suit of primitive and derived character states cited above establishes Phenacodontidae as an unambiguously delimited morphological cluster. Phenacodontids are most often confused with a few other Paleocene and Eocene placentals which I will discuss here in detail.

Arctocyonids often have higher cusps and weaker crests than phenacodontids, P_4 has a weaker talonid basin and sometimes lacks a metaconid, the paraconid of the lower molars is large and the paracristid extends more anterolabially than in phenacodontids. Lower molars also have higher trigonids. P^3 often lacks a protocone and P^4 usually has no metacone, the hypocone of the upper molars is weaker than in phenacodontids and the upper molars lack a mesostyle. Known arctocyonids have a mandibular tooth comb (Rose

and Walker, 1981), whereas phenacodontid incisors are spatulate.

Following Cifelli (1983), but unlike West (1976), I exclude *Desmatoclaenus* Gazin, 1941, from Phenacodontidae. *Desmatoclaenus* is poorly known: only fragments of the dentition and no cranial or postcranial material are known. In known characters *Desmatoclaenus* differs from phenacodontids. The talonid basin of P_4 is absent and the trigonid basin is weak in *Desmatoclaenus,* the lower molar paraconid is large, the metacone of P^3 and P^4 is absent, and the hypocone of the upper molars is weak. *Desmatoclaenus* may be structurally intermediate between arctocyonids and phenacodontids in having low bunodont crowns and partially molarized P_4, but it shares these characters with other arctocyonids, and its affinities cannot be evaluated until Arctocyonidae is revised.

Van Valen (1978) and Prothero et al. (1988) suggested close relationship between phenacodontids and *Meniscotherium.* In contrast to phenacodontids, *Meniscotherium* has high crowned, lophodont teeth, reduced anterior premolars, high entoconids, no hypoconulids, selenodont paraconules, and a large M^3. I exclude *Meniscotherium* from Phenacodontidae, although the taxon shares several derived characters with phenacodontids.

Prothero et al. (1988) included Paleocene European *Pleuraspidotherium* in phenacodontids. *Pleuraspidotherium* has only three lower premolars, the entoconid of P_4 is always present, the metastylid of the lower molars is absent, M_3 lacks a third lobe, P^3 has a large metacone, and M^3 is unreduced. In addition, *Pleuraspidotherium* is more lophodont than any phenacodontid and differs in many postcranial characters. *Pleuraspidotherium* is not a phenacodontid.

Rigby (1980) included *Tricuspiodon* in Phenacodontidae. Although similarities between phenacodontids and this taxon have been pointed out by several authors (e. g., D. E. Russell, 1980), *Tricuspiodon* differs from phenacodontids in having simple premolars.

Eocene perissodactyls are more lophodont than phenacodontids (Gingerich, 1989; McKenna et al., 1989). Transverse lophs are never developed in phenacodontid teeth, and longitudinal lophs are rarely developed. In contrast to phenacodontids, the protoconid and metaconid of P_3 of perissodactyls are approximately equally large, the lower molar trigonid basin is more open lingually, and a hypolophid connects the hypoconid with the entoconid, but not with the hypoconulid. M_3 is elongate in early perissodactyls, and the hypocone of the upper molars is as large as the protocone. The upper molars have transverse crests, and no mesostyle in primitive forms. M^3 is posteriorly little or not reduced.

Tetraclaenodon Scott, 1893

Protogonia Cope, 1881b, p. 492; Cope, 1885, p. 424; Cope, 1890, p. 359.
Tetraclaenodon Scott, 1893, p. 299; Matthew, 1937, p. 187; West, 1976, p. 13.

Euprotogonia Cope, 1893, p. 378 (footnote in Earle, 1893); Osborn and Earle, 1895, p. 64; Matthew, 1897, p. 303.

Type of genus.—*Mioclaenus floverianus* Cope, 1890.

Referred taxa.—*T. puercensis* (Cope, 1881b) and *T. septentrionalis*, new.

Age and distribution.—Torrejonian land-mammal age, western North America.

Diagnosis.—*Tetraclaenodon* differs from *Phenacodus* in lacking a mesostyle on upper molars. *Tetraclaenodon* is more bunodont than *Ectocion*, its P^1 is single rooted, and the paracristid ends high on the metaconid. *Tetraclaenodon* differs from *Copecion* in having short premolars and lacking the mesostyle.

Description.—*Tetraclaenodon* is a bunodont phenacodontid, and its lower premolars have a high protoconid. The metaconid of P_3 is weak and its trigonid basin narrow. The metastylid and protostylid of P_4 are often absent. The paraconid of the lower molars is usually present, and the paracristid ascends the metaconid. P^3 has a small protocone. P^4 is short, with weak conules, the metacone is small and proximate to the paracone. The mesostyle of upper molars is small or absent. The mandibular symphysis is unfused.

Discussion.—I exclude *Tetraclaenodon minor* (Matthew, 1897) from *Tetraclaenodon*. Matthew (1937) and West (1976) referred specimens of the taxon to *Tetraclaenodon* on the basis of the morphology of permanent molars and deciduous premolars. In addition to these, permanent premolars are also present in the type specimen (AMNH 3896), but these remained unprepared until recently. Preparation of the P_3, P_4, and P^4 shows that these teeth resemble arctocyonids more closely than phenacodontids. P_4 lacks a trigonid basin and metaconid, and P^4 lacks a metacone. On the upper molars, the mesostyle is absent. Only two specimens have been referred to the taxon: AMNH 3897 and 3904. AMNH 3897 consists of remains of several individuals and was referred to *Protogonia zuniensis* by Cope, 1890. The three specimens of "*Tetraclaenodon*" *minor* pertain to an arctocyonid.

Simpson (1937b) and West and Baird (1970) discussed the suppression of *Protogonia* and the genotype *P. subquadrata*. *Protogonia* was held for a homonym of *Protogonius* Huebner, 1819, by Cope (in Earle, 1893). Cope's view was accepted by most authors, although *Protogonia* and *Protogonius* are not homonyms according to the Code of Zoological Nomenclature. *Protogonia* is therefore a senior synonym of *Tetraclaenodon*. West and Baird (1970) proposed to suppress *Protogonia* because the name has been in disuse since 1893. The International Commission for Zoological Nomenclature has apparently never acted on this case.

Scott (1893) is the author of the name *Tetraclaenodon* and proposed a taxon referred to *Mioclaenus, M. floverianus*, as its type. Although Scott's generic name is generally accepted for the taxon, Cope's (1881b) original specific indication has priority: *T. puercensis*.

Tetraclaenodon puercensis (Cope, 1881)
Fig. 3

Phenacodus puercensis Cope, 1881b, p. 493; Cope, 1885, p. 488, pl. 25e:12–13, 57f:8–9.
Protogonia subquadrata Cope, 1881b, p. 493; Cope, 1885, pl. 57f:11–12.
Phenacodus wortmani (in part), Cope, 1882a, p. 179.
Protogonia plicifera Cope 1882g, p. 834; Cope, 1885, p. 424, pl. 25f:2–3.
Phenacodus calceolatus Cope, 1883, p. 561; Cope, 1885, p. 487, pl. 24g:7.
Mioclaenus floverianus Cope, 1890, p. 330.
Euprotogonia puercensis, Osborn and Earle, 1895, p. 65, fig. 19; Matthew, 1897, p. 303, fig. 12.
Tetraclaenodon symbolicus Gidley in Simpson, 1935a, p. 239; Simpson, 1937b, p. 246, fig. 70–71.
Tetraclaenodon puercensis, Matthew, 1937, p. 192, fig. 44–49, pl. 53–54; West, 1970, p. 852, fig. 1–2; West, 1971, p. 8, fig. 4a; Rigby, 1980, p. 124, pl. 11, fig. 10–15; McKenna et al., 1987, p. 35.
Tetraclaenodon subquadratus, Matthew, 1937, p. 193.
Tetraclaenodon pliciferus, Matthew, 1937, p. 193; West, 1971, p. 8, fig. 3.
Tetraclaenodon? puercensis, Winterfeld, 1982, p. 99.
Tetraclaenodon puercensis (in part), West, 1976, p. 13, fig. 34.

Holotype.—AMNH 3832, left dentary with M_{2-3}, right dentary with P_4 fragment and M_{1-3}, left maxilla with M^{1-3}. The specimen was collected by David Baldwin in 1881 from an unknown locality in the San Juan Basin and is of Torrejonian age.

Age and distribution.—*T. puercensis* is known from the *Tetraclaenodon* and *Pantolambda* zones of the Torrejonian from Williston, Crazy Mountains, Bighorn, Great Divide, Washakie, and San Juan Basins, and Laudate Canyon.

Diagnosis.—Smaller than *T. septentrionalis*. No shape differences between *T. puercensis* and *T. septentrionalis* are apparent.

Description.—The whole adult dentition except the upper incisors are known for *T. puercensis*. West (1971) described the deciduous dentition. As in all phenacodontids the paraconid of D_4 is large, and the trigonid basin shallow. D^4 has a large protocone and hypocone, and resembles a molar rather than P^4. AMNH 2468 is a partial skull and skeleton, AMNH 16653 is a fragmentary skull, and AMNH 15927 a fragmentary skeleton. These specimens were described by Matthew (1897, 1937), Osborn (1898b), and Radinsky (1966). Size is the main difference between *Tetraclaenodon puercensis* and *T. septentrionalis*, although minor differences may be present in M_3 (see discussion of *T. septentrionalis*). The absence of discrete differences probably reflects mainly our poor understanding of the morphology of *T. septentrionalis*.

Discussion.—The largest sample of *T. puercensis* is from the San Juan Basin, where the taxon ranges through the *Tetraclaenodon* and *Pantolambda* zones. Hundreds of specimens have been collected, but stratigraphic control is poor for many of these. Different authors have published
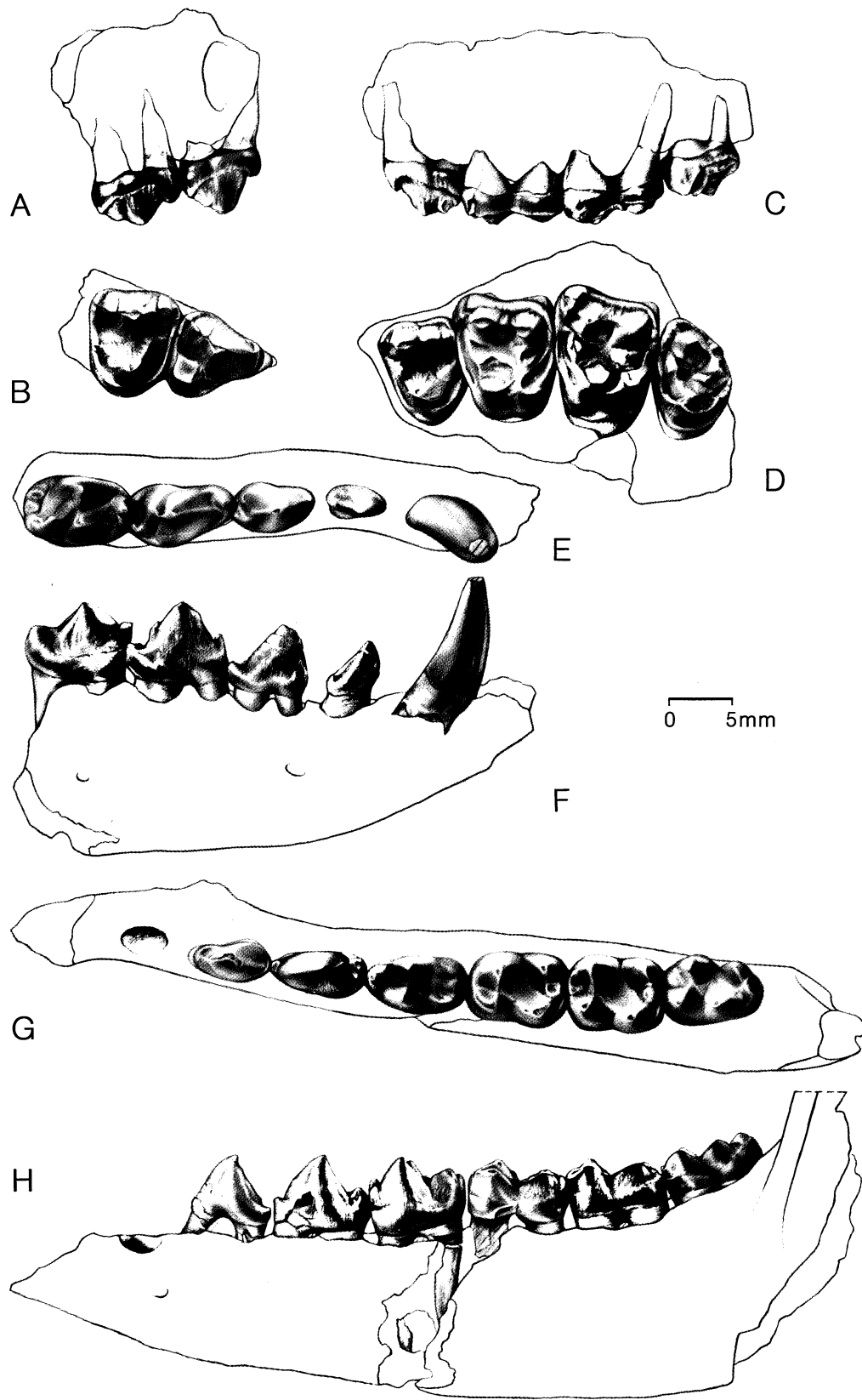
different opinions on how many lineages of *Tetraclaenodon* are present. West (1976) classified all San Juan Basin *Tetraclaenodon* as *T. puercensis,* whereas Matthew (1937) recognized four taxa. The size of the holotypes of *Phenacodus puercensis, Protogonia subquadratus,* and *Protogonia pliciferus* are within the range of one large stratigraphically constrained sample from University of Kansas locality Big Pocket. Cope (1882g) distinguished *Protogonia subquadrata* from *P. plicifera* on the basis of the morphology of the premetacrista and postmetacrista of P⁴. The present sample does not show two distinct groups. Cope (1881b) did not compare these two taxa to *Tetraclaenodon puercensis,* but stated later (Cope, 1885) that these taxa are similar. I follow most recent workers (e.g., West, 1976) and consider these taxa synonymous.

Cope (1883) used mainly characters of the cingulum to distinguish *Tetraclaenodon calceolatus* from *T. puercensis.* These characters are highly variable and are not bimodal. *T. calceolatus* is a synonym of *T. puercensis.* I distinguish *Tetraclaenodon puercensis* from the hypodigm of "*T.*" *minor,* which is not a phenacodontid.

Fig. 4 shows the size distribution for M_1 and M_2 of *Tetraclaenodon.* The locality Big Pocket is in the lower part of the Kutz Canyon section published by Lindsay et al. (1981) and yields fossils from the *Tetraclaenodon* zone. The extended right tail of the size distribution of *Tetraclaenodon* from Big Pocket is caused by a few large specimens. I interpret these specimens as large individuals of *T. puercensis.* The coefficient of variation for lengths of both M_1 and M_2 is 6.4, and thus similar to that in other mammals (Simpson et al., 1960; Long, 1968; Gingerich, 1974; Gingerich and Winkler, 1979).

Tetraclaenodon puercensis is known from a number of localities in the Crazy Mountains Basin, but only locality 25 yields more than two specimens and it forms the bulk of the specimens used in Fig. 4. The mean size of these specimens is smaller than the samples from Rock Bench Quarry of the Bighorn Basin or Big Pocket. Simpson (1937a) used smaller size as well as the geographical distance between the San Juan and Crazy Mountains Basins to distinguish the Crazy Mountains sample as a different taxon. The sample from these areas has been increased, and geographical intermediates are available now. Renewed study does not justify Simpson's distinction. I follow, among others West (1976), and synonymize *T. symbolicus* with *T. puercensis.* Simpson (1937b) listed a P_4 (AMNH 35407) from Crazy Mountains Basin locality 70 as "lower tooth probably of *Tetraclaenodon,* but possibly *Gidleyina*" (p. 39). This specimen and an upper molar fragment from the same locality (AMNH 35406) fall into the size range of *Tetraclaenodon* and are larger than most *Ectocion*

collinus (Simpson's *Gidleyina*). I refer these specimens to *Tetraclaenodon puercensis.*

Tetraclaenodon puercensis is also known from Medicine Rocks Site I (CCM 73–35, YPM-PU 19654) and Rigby (1980) described it from Swain Quarry in the Washakie Basin. The mean of the Swain Quarry sample is larger than the Big Pocket sample, and compares better to larger, younger San Juan Basin samples studied by Taylor (unpubl., 1984). This corroborates the late Torrejonian age suggested for the sample by Archibald et al. (1987).

A single specimen of *Tetraclaenodon puercensis* is known from the Laudate Fauna of the Goler Formation of California (West, 1970; McKenna et al., 1987).

Referred specimens.—Williston Basin, Torrejonian: CCM 73–35 (not seen) and YPM-PU 19654. Crazy Mountains Basin, *Pantolambda* zone: AMNH 35406, 35407, 35426–35431, UM field number 85–228, 85–398, USNM 6167, 6168, 6169 (holotype *Tetraclaenodon symbolicus*), 9925, 10074, and YPM-PU 13757; Torrejonian: CM 1006, USNM 22144, and 405035. Bighorn Basin, *Pantolambda* zone: YPM-PU 13323, 13335, 13936, 13947, 13954, 14022, 14080, 14081, 14084, 14220, 14221, 14259, 14261, 14831, 16595–16601, 17440, 17446, 17447, 17498, 17641, 17731, 18506, 18507, 18508, 18509, 18510, 18511, 18700, 18756, 19054, 19613, 19793, 20273, 20286, 20287, 20335–20342, 20345, 20349–20355, 20357, 20358, 20380–20382, 22225, UM 66128 and 75938. Great Divide Basin, Torrejonian: UW 13236. Washakie Basin, *Pantolambda* zone: AMNH 87602, 87603, 87604, 87626, 87662, 87674, 87688, 87701, 87749, 87765, 87821, 88094, 100569, 100570, 100571, and 100573. San Juan Basin, *Tetraclaenodon* zone: UK 7857, 7858–7882, 7893, 7970, 7972, 7974, 7975, 7977–7981, 8052, 9525, 9654, 9656–9672, 10574, 10578, 10579, 10580, 10581, 10624, 10630, 13459, 13460, and 13468; *Pantolambda* zone: UK 7863, 8048–8065, 9500, 9501, 13998, and 14013; Torrejonian: AMNH 3876 (holotype *Protogonia subquadrata*), 3900 (holotype *Protogonia plicifera*), UK 8023, 8028, 13999, and UM 60154. Laudate Canyon, Torrejonian: UCMP 69122.

Tetraclaenodon septentrionalis, new species
Fig. 5

Euprotogonia puercensis, Douglass, 1902, p. 222, pl. 29:6–8.
Euprotogonia sp. (in part), Douglass, 1908, p. 22, pl. 1:4, 2:12–13.
Tetraclaenodon cf. *puercensis,* Simpson, 1937b, p. 249; L. S. Russell, 1958, p. 100, pl. 1:8.

Holotype.—YPM-PU 13760, right P^3, M^{2-3}, and fragment of right M^1. The specimen was collected by E. Douglass at locality 5 of Simpson (1937b) and is from the *Pantolambda* zone of the Crazy Mountains Basin.

Age and distribution.—*Tetraclaenodon* and *Pantolambda* zones of the Tiffanian from the Crazy Mountains Basin.

Diagnosis.—*Tetraclaenodon* larger than *T. puercensis.* Lower molars possibly wider than in *T. puercensis.*

Description.—Only two P^3s, several upper molars and two lower molars are known for *Tetraclaenodon septentrionalis.* The molars of *T. septentrionalis* differ from those of *T. puercensis* by their large size. The length of M^2 of the holotype of *T. septentrionalis* is more than six standard

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Figure 3. Dentition of *Tetraclaenodon puercensis* from Rock Bench Quarry. A and B, P^{3-4} (UM 66128), labial and occlusal view. C and D, P^4-M^3 (YPM-PU 20286), labial and occlusal view. E and F, C_1-P_4 (YPM-PU 14259), occlusal and labial view. G and H, P_2-M_3 (YPM-PU 13954), occlusal and labial view.
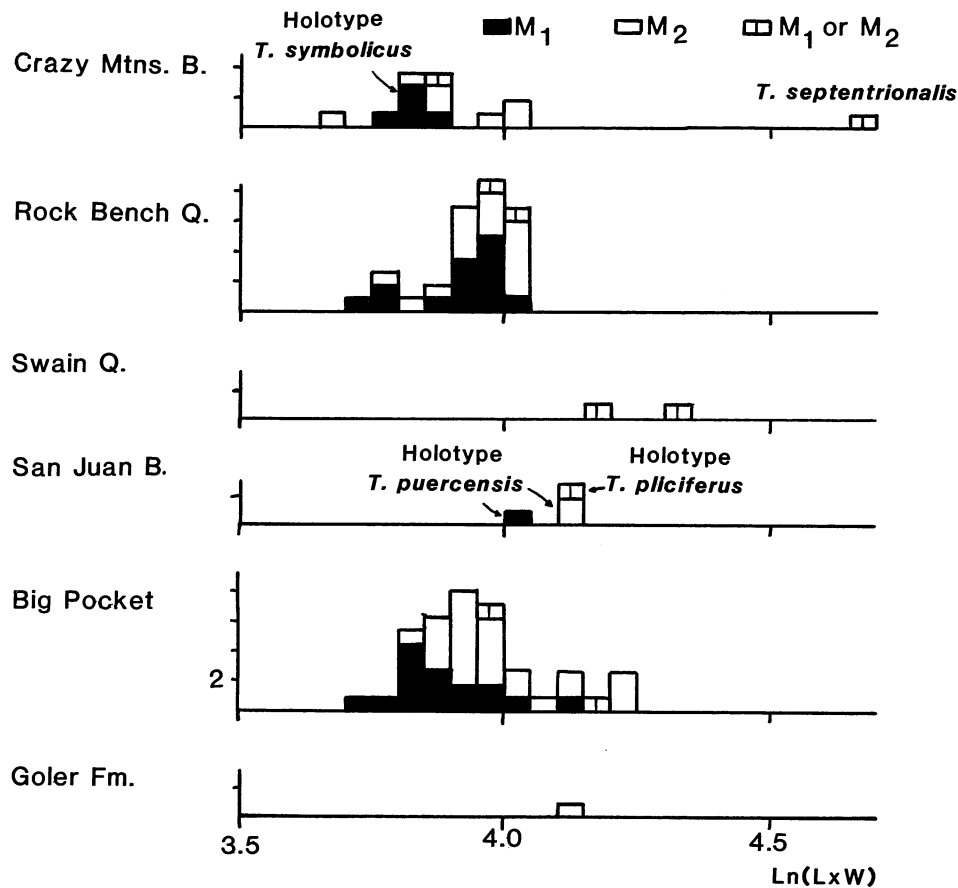
Figure 4. Histogram of natural logarithm of product of length and width for M_1 and M_2 of late Torrejonian *Tetraclaenodon puercensis* and *T. septentrionalis*. Specimens from Laudate Canyon in the Goler Formation, Big Pocket in the San Juan Basin, Swain Quarry in the Washakie Basin, and Rock Bench Quarry in the Clarks Fork Basin. Note the homogeneity in molar size for *Tetraclaenodon* from most areas, except for the large *T. septentrionalis*.

deviation units larger than the mean of the Rock Bench Quarry sample of *T. puercensis,* and its width is more than five standard deviation units larger.

Two M_3's are known for *T. septentrionalis*. They are wider and have a smaller hypoconulid than the M_3 of *T. puercensis*. The drawing of one of these (CM 1164) published by Douglass (1908) is inaccurate in several respects.

Discussion.—Tetraclaenodon septentrionalis is known only from the northern part of the geographic range of the genus, and is rarer than *Tetraclaenodon puercensis*. Stratigraphically it ranges between 800 and 1350 feet in the Crazy Mountains Basin section published by Simpson (1937b). It is known from Gidley Quarry, and Simpson's (1937b) localities 6, 25, and 82. The range of *Tetraclaenodon puercensis* in the Crazy Mountains Basin extends before and after this. Only a few specimens of the taxon are known and this was probably the reason why the taxon was

not named previously, although Douglass (1908) noticed differences from *T. puercensis*.

Tetraclaenodon septentrionalis is not known from Rock Bench Quarry in the Bighorn Basin. Gingerich (1976a) stated that the Rock Bench Quarry fauna postdates the Gidley Quarry fauna. Rock Bench Quarry is possibly equivalent in time to the later Torrejonian levels of the Crazy Mountains Basin, postdating the disappearance of *T. septentrionalis*. Except for one locality, *T. septentrionalis* is only known from sites at which *T. puercensis* was also recovered.

I also refer an isolated lower molar from the Alberta Syncline to *T. septentrionalis*. L. S. Russell (1958) described the specimen (NMC 9105), which agrees with the M_3 from the type area in being larger and wider than other *Tetraclaenodon*.

Etymology.—septentrionalis, Latin for northern. The

0   5mm
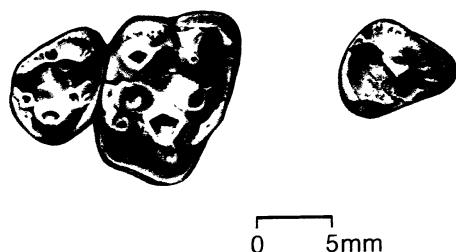
Figure 5. Dentition of *Tetraclaenodon septentrionalis* from Crazy Mountain Basin, locality 5. P³, M²⁻³ (YPM-PU 13760), holotype in occlusal view. Lower molar fragment included in holotype is not figured.

taxon is only known from the northern part of the range of *Tetraclaenodon*.

Referred specimens.—Alberta Syncline, Torrejonian: NMC 9105 (not seen). Crazy Mountains Basin, *Pantolambda* zone: AMNH 35424, 35425, 35725, 35726, CM 1016, 1164, and USNM 9620.

Ectocion Cope, 1882

Oligotomus (in part), Cope, 1882a, p. 182.
Ectocion Cope, 1882c, p. 522; Cope, 1885, p. 695; Granger, 1915, p. 348; West, 1976, p. 46.
Gidleyina Simpson, 1935a, p. 240.
Prosthecion Patterson and West, 1973, p. 2; West, 1976, p. 44.

Type of genus.—*Oligotomus osbornianus* Cope, 1882a.

Referred taxa.—*E. parvus* Granger, 1915; *E. superstes* Granger, 1915; *E. collinus* L. S. Russell, 1929; *E. major* (Patterson and West, 1973); *E. cedrus* new; and *E. mediotuber*, new.

Age and distribution.—Tiffanian through early Bridgerian land-mammal ages of western North America.

Diagnosis.—Most lophodont phenacodontid. Differs from all other phenacodontids in the large parastyle and mesostyle of the upper molars. P¹ double rooted or with one elongate root and M³ without hypocone, unlike *Tetraclaenodon* and *Phenacodus*. Differs from *Copecion* in the short P₄, P³ and P⁴.

Description.—*Ectocion* is more lophodont than any other phenacodontid. The shape of the metacristid is one of the best indicators of lophodonty. The metacristid of *Ectocion* usually has the shape of an open U in posterior view. The convexity of the cusps of other phenacodontids causes the metacristid to converge in a narrow valley, it is V-shaped. The paracristid of the molars ends low on the paraconid in most individuals of late Tiffanian and younger *Ectocion*, but not in many *Ectocion collinus*. The paraconid is usually absent. The parastyle and mesostyle of the upper molars are large and are connected by a W-shaped ectoloph. Occasionally the mesostyle is small, such as in the holotype M³ of *Ectocion collinus*. This specimen is also one of the few *Ectocion* with a hypocone on M³. The mesostyle is also absent in an M³ of *E. mediotuber* from the Clarks Fork Basin (YPM-PU 18965). The hypocone of

M¹ and M² is smaller than in other phenacodontids, and it is usually absent in M³, but present in an M³ of *E. cedrus* from Cedar Point Quarry (YPM-PU 20291).

Overall size and shape characters of the premolars distinguish best between different *Ectocion*. In general, members of the genus differ by degrees of inflation of protoconid and hypoconid of P₃ and the size of the metaconid.

Based on the little non-dental material available for *Ectocion*, differences from *Phenacodus* include the narrow rostrum with inflated preorbital regions. As in *Phenacodus*, the mandibular symphysis can be fused or unfused. *Ectocion* is probably more cursorial than *Phenacodus* (see Chapter V) .

Discussion.—A specimen of *Ectocion* was first described by Cope (1882a), who referred it to a perissodactyl genus that he created in 1873b: *Oligotomus*. Cope (1882c) referred *Oligotomus osbornianus* to the new genus *Ectocion*, but he never discussed the etymology of the generic name. It is apparently composed of the latinized version of the Greek words *ekto* (outer) and *kioon* (column), a reference to the prominent mesostyles of *Ectocion*.

The synonymy of *Gidleyina* and *Ectocion*, as discussed by West (1976), is generally accepted. I here also synonymize *Prosthecion* and *Ectocion*. The sample used in all previous discussions of *Prosthecion* consists of lower molars of several individuals, but of only two P₄s, a single P₃ and the upper cheek teeth of one individual. Patterson and West (1973) as well as West (1976) mainly used the characters of upper premolars and P₃ of the holotype to diagnose the monotypic genus *Prosthecion*, and could therefore not take variation within the taxon into account.

Based on the variation in *Ectocion osbornianus*, many differences cited in the diagnosis of *Prosthecion major* Patterson and West, 1973, can be attributed to individual variation, such as the size of the cingulum of the upper molars. The size of stylids in P₃ and P₄ and the width of the talonid of P₄ are variable in *Ectocion* and similar to *Prosthecion*. The entoconid of P₄ is absent in *Prosthecion* as well as in many *Ectocion*, and the position of the hypoconid is variable. No difference between paracone and metacone of P³ is apparent; a separate paracone and metacone are present in *E. osbornianus* as well as in the holotype of *Prosthecion major*. The width of P³ cannot be evaluated in the holotype of the latter, because its lingual side is not preserved. Patterson and West (1973) state correctly that *Prosthecion* and *Ectocion* are similar in the upper molars. Morphological differences between *Prosthecion major* and *Ectocion osbornianus* are not larger than those between any other pair of taxa referred to *Ectocion*, and I therefore consider *Prosthecion* a junior synonym of *Ectocion*.

Ectocion collinus Russell, 1929
Figs. 6 and 7

Ectocion collinus L. S. Russell, 1929, p. 177, fig. 4; Gingerich, 1982a, fig. 1; Krause and Gingerich, 1983, p. 178, figs. 15–16.
Meniscotherium semicingulatum L. S. Russell, 1929, p. 178, fig. 5.
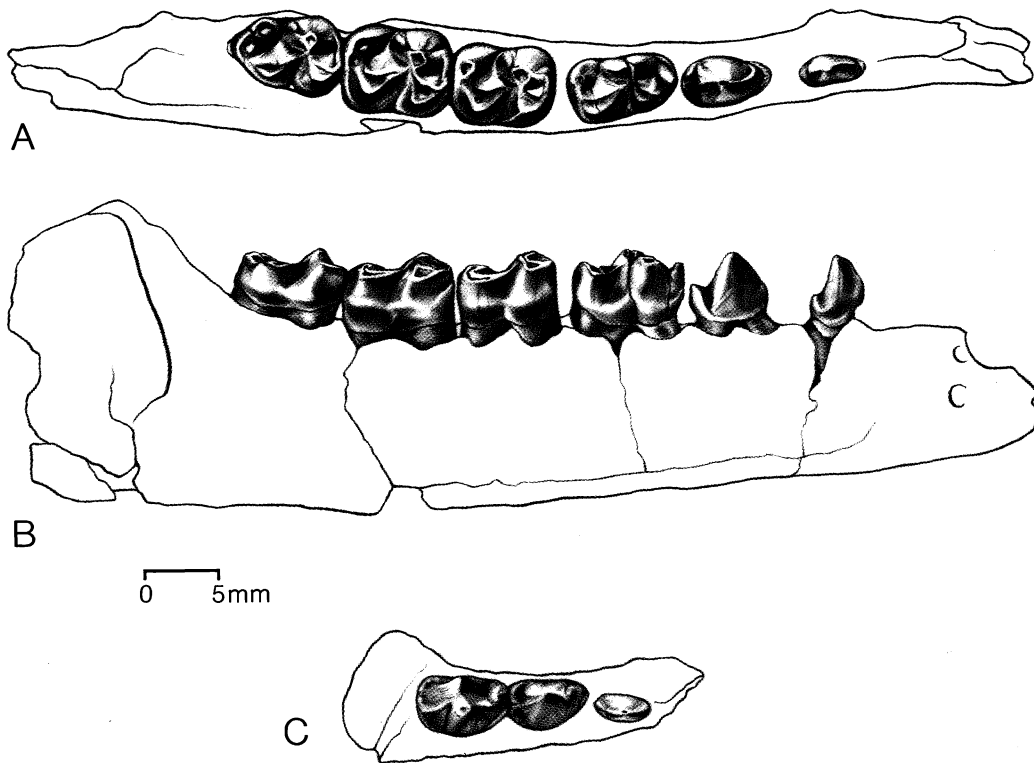
Figure 6. Dentition of *Ectocion collinus*. A and B, P₂-M₃ (YPM-PU 14961) from Jepsen Quarry in occlusal and labial view. C, P₂₋₄ (UM 88985) from Douglass Quarry in occlusal view.

?Tetraclaenodon superior Simpson, 1935a, p. 239.

Gidleyina montanensis Gidley in Simpson, 1935a, p. 240; Simpson, 1937b, p. 251, fig. 72.

?Gidleyina silberlingi Gidley in Simpson, 1935a, p. 240; Simpson, 1937b, p. 253, fig. 73.

?Gidleyina superior, Simpson, 1937b, p. 254, fig. 74.

Ectocion sp., Gazin, 1942, p. 220.

Gidleyina wyomingensis Gazin, 1956a, p. 42, pl. 9.3–4.

Gidleyina? cf. *G. wyomingensis*, Dorr, 1958, p. 1224.

Gidleyina? near *G. wyomingensis*, Gazin, 1956b, p. 710.

Ectocion montanensis, West, 1971, p. 22, fig. 16; West, 1976, p. 47, fig. 30.

Ectocion wyomingensis, West, 1971, p. 22, fig. 17; Holtzman, 1978, p. 59, figs. 11.12–18.

Ectocion wyomingensis (in part), West, 1976, p. 48, fig. 32.

Phenacodus vortmani (in part), West 1976, p. 30.

Ectocion sp. cf. *E. wyomingensis* (in part), Winterfeld, 1982, p. 100.

Holotype.—UA 118, partial right M³, "locality I, Cochrane" (L. S. Russell, 1929), Alberta Syncline, Canada. This locality yields early Tiffanian fossils, possibly from the *P. praecursor* zone (Krause, pers. comm., 1988).

Age and distribution.—*Plesiadapis praecursor* through *Plesiadapis rex* zone of the Tiffanian of the Alberta Syncline and Williston, Crazy Mountains, Bighorn, Green River, Fossil, Bison, and Washakie Basins.

Diagnosis.—*Ectocion collinus* is larger than *E. cedrus*, and comparable in size to *E. mediotuber*. P₃ metaconid always absent, unlike all other *Ectocion*. Hypoconid smaller than in *E. mediotuber* and later *Ectocion*. Paracone and metacone of P⁴ proximate, unlike all other *Ectocion*.

Description.—Only dental material is known for *E. collinus;* it includes P₂ to M₃, P² to M³, D₃₋₄, and D³⁻⁴. The deciduous dentition of *E. collinus* was described by West (1971). *E. collinus* is larger than middle and late Tiffanian *E. cedrus* (Fig. 8), and similar in size to late Tiffanian *E. mediotuber*. The main shape differences between *E. collinus* and these taxa are absence of a metaconid on P₃ and the proximate protocone and metacone of P⁴. P₃ of *E. collinus* is relatively longer than in *E. cedrus*, and comparable in length to *E. mediotuber* (Table 2). The entoconid of P₄ is present in 24% of specimens (N=25), and the talonid of P₄ is narrow. The parastyle of P³ is small and the paracone and metacone of P⁴ are proximate. The mandibular symphysis is unfused.

Discussion.—The holotype M³ of *E. collinus* is unusual in several respects: it is larger than most specimens, has a small mesostyle and the hypocone is present. The aberrant morphology of the specimen led West (1976) to synonymize the taxon, then based on the holotype only, with *Phenacodus vortmani*. The lophodonty of the specimen in-

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0            10mm
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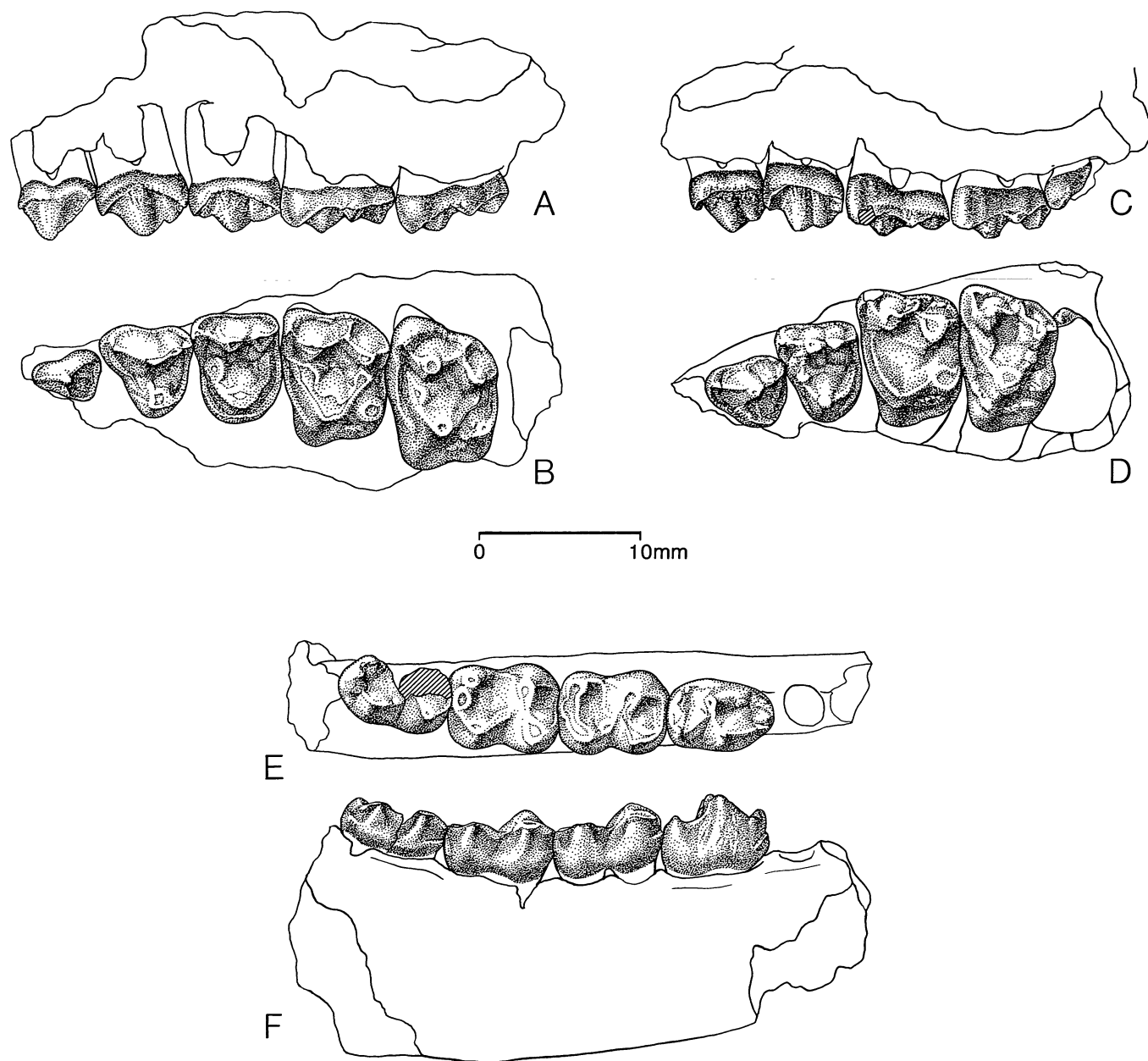
Figure 7. Dentition of *Ectocion collinus*. A and B, P^2-M^2 (YPM-PU 12048), part of holotype of "*Gidleyina montanensis* Simpson" from Crazy Mountains Basin locality 68 in labial and occlusal view. C and D, P^3-M^2 (YPM-PU 14604) from Douglass Quarry in labial and occlusal view. E and F, P_4-M_3 (YPM-PU 14603) from Douglass Quarry in occlusal and labial view. Reprinted from Krause and Gingerich (1983), drawings by Karen Klitz.

dicates that the specimen is referable to *Ectocion* as pointed out by Gingerich (1982a). Two more specimens of *E. collinus* are known from locality Cochrane 2 near the type locality, a D_4 (UA 120) and a P^2 (UA 121). These two specimens are the hypodigm of *Meniscotherium semicingulatum* L. S. Russell, 1929, and were included in *E. collinus*

by Gingerich (1982a). The size of these two specimens matches that of *E. collinus* from the Crazy Mountains Basin and the Bison Basin, indicating that the holotype is unusually large even for specimens collected in the Alberta Syncline. The age of these specimens is early Tiffanian (Fox, 1988).
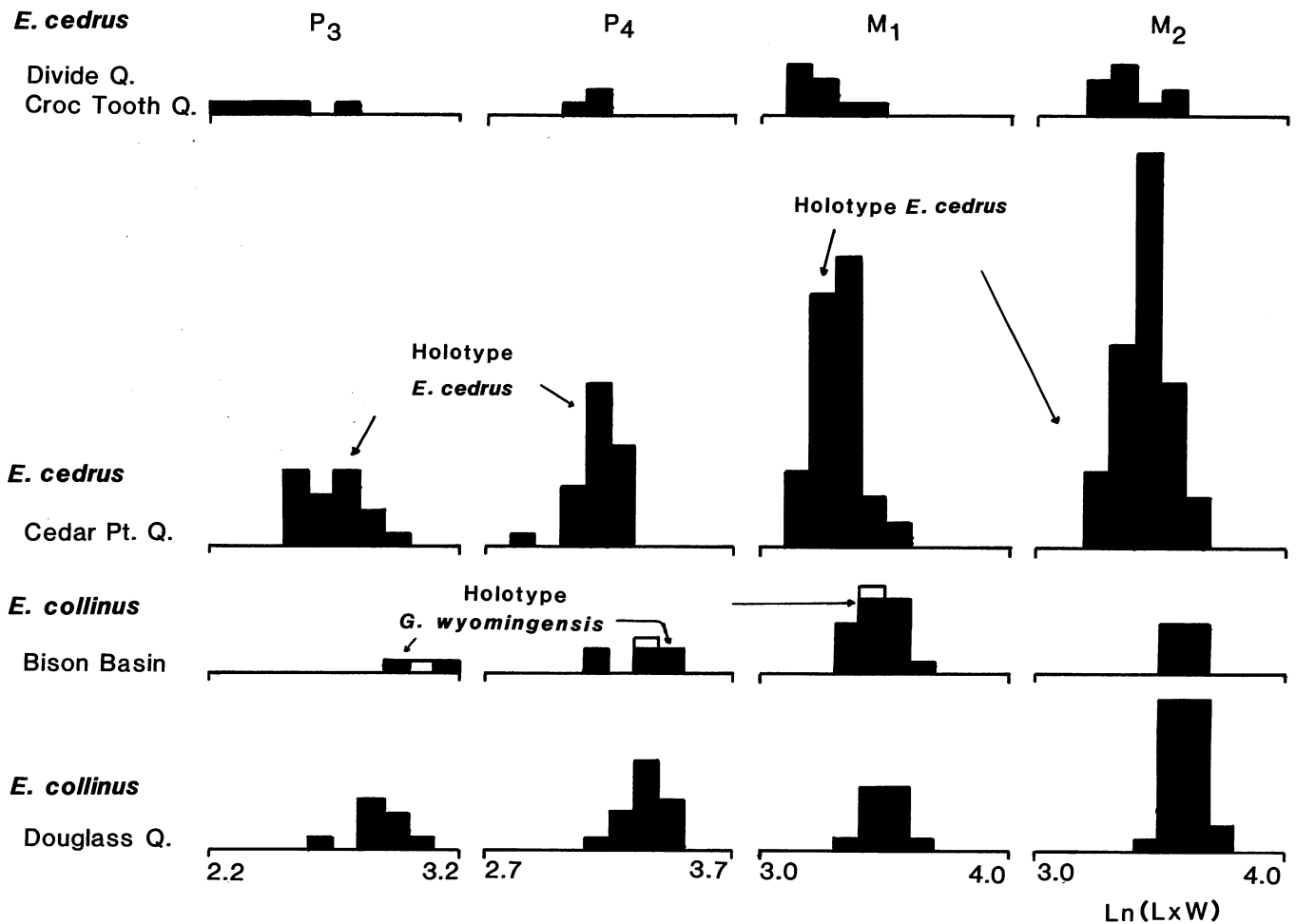
Figure 8. Histograms of natural logarithm of product of length and width (in mm) for P_3 through M_2 in some Tiffanian *Ectocion*. From bottom to top: *Ectocion collinus* from Douglass Quarry, *Plesiadapis praecursor* zone; *Ectocion collinus* from pooled Bison Basin localities, *P. anceps* zone (white) and *P. rex* zone (black); *Ectocion cedrus* from Cedar Point Quarry, *P. rex* zone; *Ectocion cedrus* from Croc Tooth Quarry and Divide Quarry, *P. churchilli* zone.

Table 2. Ratios of lengths of associated cheek teeth in
Ectocion and *Copecion*.

Taxon	P_3/P_4			P_3/M_1		
	N	Mean	SD	N	Mean	SD
E. collinus	7	0.87	0.05	5	0.87	0.03
E. cedrus	17	0.82	0.08	19	0.81	0.06
E. mediotuber	4	0.88	0.05	5	0.90	0.04
E. osbornianus	126	0.99	0.06	82	1.02	0.07
E. parvus	3	1.00	0.08	2	1.06	0.07
C. brachypternus	22	0.92	0.07	18	1.07	0.09
C. davisi	1	0.90	—	1	1.03	—

Simpson (1935a, 1937b) divided Crazy Mountains Basin *Ectocion* into three species, mainly on the authority of an earlier manuscript by Gidley. Two of these taxa (*?Gidleyina silberlingi* and *?G. superior*) were based on only one specimen, and Simpson (1937b) expressed some doubt about the validity of *?G. silberlingi*. Gazin (1956a) suggested that these three taxa were synonymous, and he was followed by all subsequent authors.

The largest collections of *Ectocion collinus* are from the Crazy Mountains and Bison Basins. Most authors have followed West (1976) in referring *Ectocion* specimens from the Crazy Mountains Basin to *E. montanensis*, and specimens from the Bison Basin to *E. wyomingensis*. Gazin (1956a) originally diagnosed *Gidleyina wyomingensis* as distinct from the specimens from the Crazy Mountains Basin on the basis of the small P_3, shallow molar trigonid, weak molar paraconid, and larger mesostyles. On the basis of a larger sample, West (1976) rejected most of these differences but stressed two characteristics distinguishing *Ectocion montanensis* from *Ectocion wyomingensis*: the size of the paraconid of the lower molars and the position

of the hypoconulid. Some lower molars (e.g., YPM-PU 14603) in the *E. collinus* sample from Douglass Quarry lack a paraconid, which is in contrast to West's (1976) claim that this cusp is always present in *E. montanensis*. The development of the paraconid does not differ between samples of *E. wyomingensis* and *E. montanensis* and differences in the distance between hypoconulid and hypoconid are also not apparent to me. None of the characters that have been used to distinguish *E. collinus* from *E. wyomingensis* differentiate consistently between these taxa and I therefore synonymize these taxa.

Holtzman (1978) described *Ectocion* specimens from Brisbane and Judson in the Williston Basin. The specimens are larger than *Ectocion cedrus*, and judging from Holtzman's figure (1978:11.12), it seems that the parastyle of a P3 in the collection (SMM P77–8–199) is small. These two characters indicate that the specimens are referable to *E. collinus* rather than to *E. mediotuber*, and corroborates that these faunas are middle Tiffanian or older.

Only three specimens of *Ectocion collinus* are known from the Bighorn Basin. This is probably due to the sporadic occurrence of fossils in the early Tiffanian of the Bighorn Basin. One of these (YPM-PU 20856) has a high protoconid and metaconid in P_4. This tooth is hardly worn, while dentine is broadly exposed in M_1. It differs in this respect from typical *Ectocion*: usually P_4 and M_1 are similar in wear stage. Another Bighorn Basin specimen of *E. collinus* (YPM-PU 14961) was found at Jepsen Quarry, where *E. cedrus* is also found.

Referred specimens.—Alberta Syncline, *Plesiadapis praecursor* zone: UA 120 (holotype *Meniscotherium semicingulatum*) and 121. Williston Basin, Tiffanian: SMM P77–8–199 (not seen). Crazy Mountains Basin, *Plesiadapis praecursor* zone: UM 80827, 84558–84600, 84603–84625, 84627–84631, 88956–88959, 88961, 88962, 88964–88990, 88992–89067, and USNM 6166 (holotype *?Gidleyina silberlingi*), YPM-PU 12048 (holotype *Gidleyina montanensis*), 14603–14611, and 20417–20435; *Plesiadapis rex* zone: UM field number 85–318, 85–319, 85–328, 86–146, 86–148, and USNM 11913 (holotype *Tetraclaenodon superior*). Bighorn Basin, Tiffanian: UM 58125, YPM-PU 14961, and 20856. Wind River Basin, *Plesiadapis praecursor* zone: CM 15951, 18165, UCM 23333, 23405, 23411, and 25331. Green River Basin, *Plesiadapis rex* zone: CM 8808, 8815, 8820, 8826, UM 34777–34780, 69543, 80801, USNM 214538, USNM field number 25–63, and 59–64. Fossil Basin, *Plesiadapis rex* zone: USNM 21264, 406120, and 406121. Bison Basin, *Plesiadapis anceps* zone: AMNH 92102, CM 18731, 18732, 18757, UCM 40308, 40414, 40431, 40444, and 40445; *Plesiadapis rex* zone: CM 40514, MCZ 18734, UCM 47470, USNM 20570, 20790 (holotype *Gidleyina wyomingensis*) 20791–20795, 405054–405062, and 405064–405068; Tiffanian: CM 40570, UCM 40310, USNM 21024, and 405075. Washakie Basin, Tiffanian: UW 13250 and 13251.

Ectocion cedrus, new species
Fig. 9

?Phenacodus, Simpson, 1927, p. 7, fig. 7.
Ectocion wyomingensis (in part), West, 1976, p. 48.

Holotype.—UM 82085, left dentary with P_2 to M_3 and alveoli for C_1 and P_1 from Cedar Point Quarry, Bighorn

Basin. Cedar Point Quarry produces fossils from the *Plesiadapis rex* zone (Gingerich, 1976a).

Age and distribution.—*Plesiadapis rex* and *P. churchilli* zones of the Tiffanian of the Alberta Syncline, and Williston, Bighorn, and Wind River Basins.

Diagnosis.—*Ectocion cedrus* is smaller than any other *Ectocion* except *E. parvus*. Premolars are relatively smaller than molars, unlike other *Ectocion*. P_3 hypoconid weak and paraconid high, unlike *E. mediotuber*. P_3 metaconid present and P4 paracone and metacone distant, unlike *E. collinus*.

Description.—C_1, P_2-M_3, C^1, P^3-M^3, D_{2-4}, and D^{2-4} are known for *E. cedrus*. *E. cedrus* differs from other *Ectocion* by its small overall size and several premolar characters. Size differences are apparent in absolute size while ratios of premolar and molar measures are also lower in *E. cedrus* (Table 2). I tested differences in means with t-tests on the more or less contemporaneous samples of Cedar Point Quarry *E. cedrus* and Bison Basin *E. collinus* for the length and width dimensions of P_3-M_2. Differences were significant in all values except M_2 length (P < .05: length P_3, P_4, and M_1; P < .001: width P_3, P_4, M_1 and M_2).

The metaconid of P_3 is present in *E. cedrus* but not in *E. collinus*. The hypoconid of P_3 is distinct but small in contrast to *E. mediotuber* and *E. osbornianus*, and its labial cingulum is present. The paraconid of P_4 is usually higher than in *E. mediotuber*. The talonid of P_4 is narrow, paraconid and metaconid are proximate, and the entoconid is usually present. P^3 has a small parastyle, in contrast to many later *Ectocion*. The mandibular symphysis is unfused in *Ectocion cedrus*.

Early Wasatchian *Ectocion parvus* is similar in molar size to *E. cedrus*. These two taxa are best distinguished on the basis of P_3, which is relatively small and has a small hypoconid in *E. cedrus* (Table 2). The entoconid is present in 82% of the P_4's of *E. cedrus* (N = 28) but in only 17% of the specimens of *E. parvus* (N = 17).

I investigated apparent differences between the Bighorn Basin samples of upper molars of *E. cedrus* and *E. parvus* by means of discriminant function analysis on the length and width of M^1 and M^2. The first discriminant function is: 5.7(length of M^1) - 2.1(width of M^1) + 0.8(length of M^2) + 2.1(width of M^2). The difference between the score means of the taxa on this function is significant at p = 0.02. The scores for the specimens on which these measurements could be taken and the posterior probabilities (probability of being classified by the function as *E. cedrus*) are summarized in Fig. 10. M^1 of *E. cedrus* is longer and narrower, and M^2 is wider than in *E. parvus*.

Discussion.—*E. cedrus* shows a change in size over time. The lower premolars of the specimens from the *Plesiadapis rex* zone are significantly larger than those of their successors from the *P. churchilli* zone, although their ranges overlap. One mandible from Cedar Point Quarry (YPM-PU 20884) has an anomalously small P_4, extending the size range for the *Plesiadapis rex* zone of P_4 below that of the *Plesiadapis churchilli* sample.
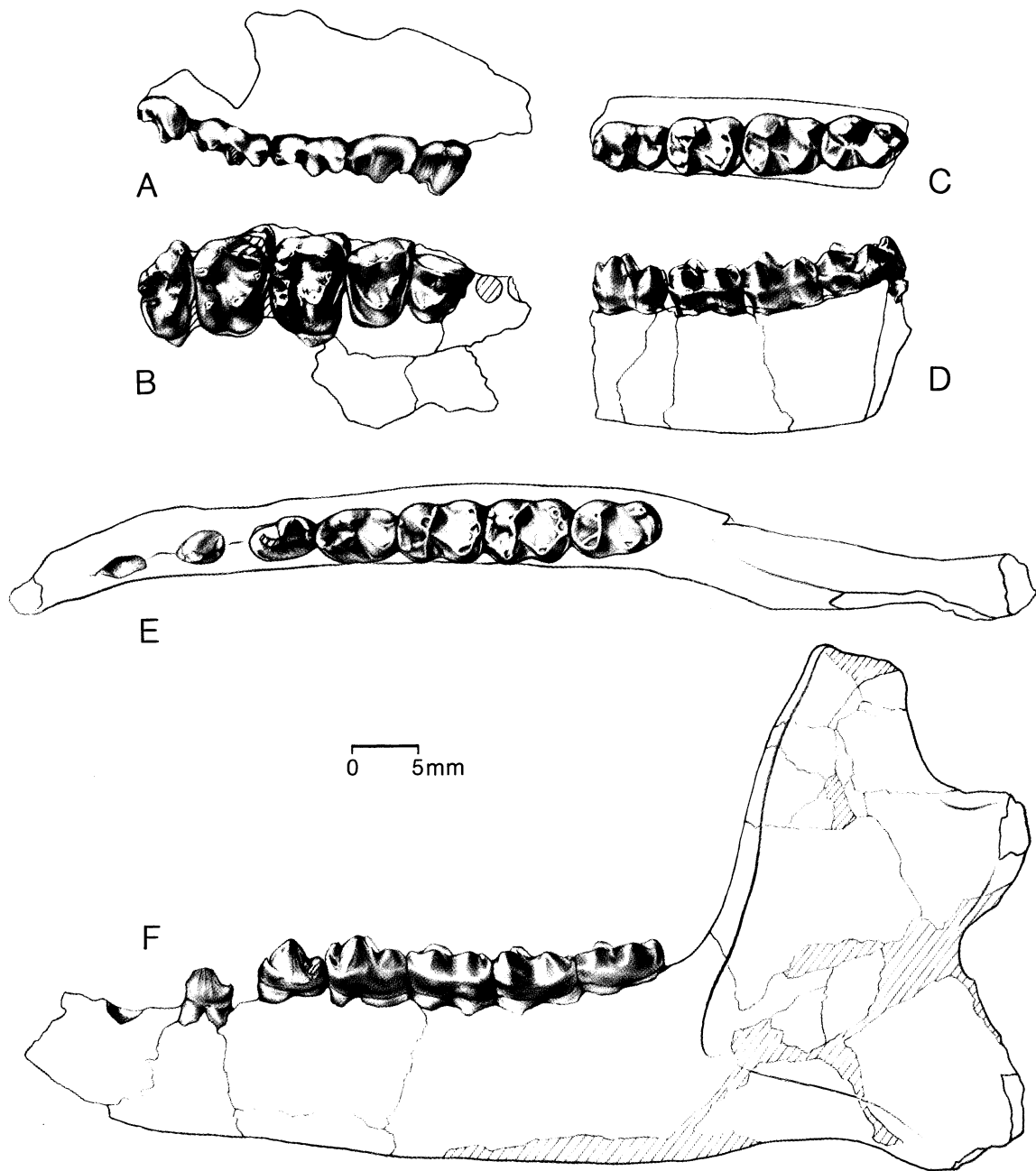
Figure 9. Dentition of *Ectocion cedrus*. A and B, P^3-M^3 (UM 85402) from Divide Quarry, labial and occlusal view. C and D, P_4-M_3 (YPM-PU 14968) from Croc Tooth Quarry in occlusal and labial view. E and F, P_2-M_3 (UM 82085), holotype from Cedar Point Quarry, in occlusal and labial view.

The sample of *E. cedrus* from Cedar Point Quarry is the largest sample of jaws of any phenacodontid from a single locality (N = 137). Paleontological samples from populations from single localities are commonly assumed to be random, and therefore normally distributed. To investigate if this assumption holds, a variant of the Kolmogorov-Smirnov test (Lilliefors, 1967) was executed on 22 variables with more than ten cases. P-values were smaller than 0.05 for five variables: normality had to be rejected for length and width of P_3, length of P_4, and length of trigonid basin of M_2 and M_3. I cannot evaluate the importance of this deviation from normality.
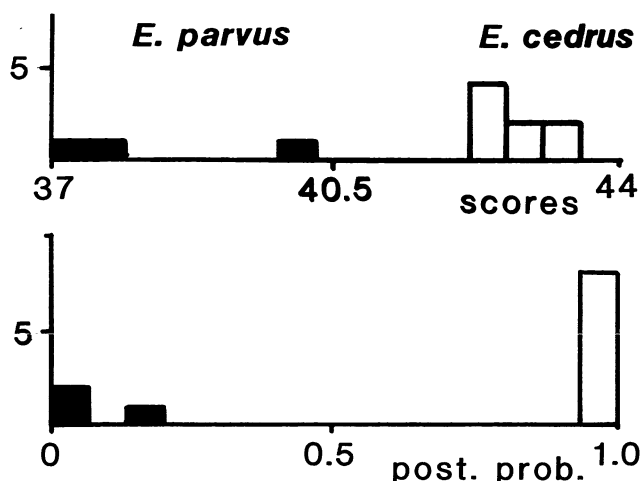
Figure 10. Histogram of results of discriminant function analysis of associated M^{1-2}s of *Ectocion cedrus* and *E. parvus*. Top diagram displays scores of specimens on first canonical discriminant function listed in text (black, *E. parvus*; white, *E. cedrus*). Bottom diagram displays probability for known specimen of being classified as *E. cedrus* by the function (posterior probability).

E. cedrus is mainly known from four sites in the eastern Bighorn Basin: Cedar Point, Croc Tooth, Divide, and Jepsen Quarries. A P_3 of *E. cedrus* (UM 73399) indicates that the taxon was also present in the floodplain deposits of the Clarks Fork Basin. *Ectocion cedrus* is known from the *Plesiadapis rex* zone between 280 and 335 m in the Clarks Fork Basin section.

Early to middle Tiffanian *E. collinus* and middle to late Tiffanian *E. cedrus* occur together at only one locality in the Bighorn Basin: Jepsen Quarry. Nearby Cedar Point Quarry has yielded thousands of fossils from the same zone, but has never produced a specimen of *E. collinus*. On the other hand, *E. cedrus* has never been recovered in the *Plesiadapis rex* zone of the Crazy Mountains and Bison Basins. It is possible that the fauna from Cedar Point Quarry postdates that from Jepsen Quarry and the extinction of *E. collinus*. The Bison Basin faunas would then also predate the Cedar Point Quarry fauna.

Ectocion cedrus and *E. mediotuber* both occur in sediments from the *Plesiadapis churchilli* zone. The fact that no *Plesiadapis churchilli* zone locality yields both *Ectocion* species can be explained in at least two ways: the taxa may be separated (1) in time or (2) in depositional environment. Most specimens of *E. mediotuber* were recovered from floodplain deposits, whereas specimens of *E. cedrus* usually come from quarry deposits.

Simpson (1927) described an M_3 (AMNH 15534 J) and fragmentary upper molar or deciduous premolar (AMNH 15534 K) from Erickson's Landing in the Alberta Syncline. This locality is considered to yield fossils from the *Ple-*

siadapis rex zone (Gingerich, 1976a). Simpson (1927) described the specimens as "*?Phenacodus*," but both specimens are without doubt *Ectocion*. On the basis of the small size of AMNH 15534 K, I refer these specimens to *E. cedrus*.

E. cedrus is also known from the White Site of the Williston Basin (YPM-PU 23687) and the taxon constrains the age of this locality to *Plesiadapis rex* or *P. churchilli* zone. It is also known from Long Draw Quarry in the Clarks Fork Basin.

Middle Tiffanian Love Quarry in the Togwotee Pass area of the Wind River Basin has produced several specimens that I refer to *E. cedrus*. A maxilla with P^4-M^3 (AMNH 88259) agrees with *E. cedrus* in morphology of P^4, but is smaller than Cedar Point Quarry specimens. Additional isolated molars agree well in size with Bighorn Basin *E. cedrus*.

Etymology.—Cedrus (Latin: cedar), named for the coniferous trees, junipers, locally called cedars, that gave their name to the type locality, Cedar Point Quarry.

Referred specimens.—Alberta Syncline, *Plesiadapis rex* zone: AMNH 15543 J and 15543 K. Powder River Basin, Tiffanian: YPM-PU 23687. Bighorn Basin, *Plesiadapis rex* zone: UM 63096, 63096, 64397, 64398, 64401, 64408, 64418, 64447, 64450, 64451, 64506, 64511, 64512, 64522, 64527, 64556, 64563, 64633, 71827, 71829, 73397, 73399, 73706, 82064, 82089, 82094, 83046, 83258, YPM-PU 14960, 14963, 17792, 17778–17782, 19557, 19565, 19568, 19575, 19583, 19588, 19591, 19626, 19918, 19932, 19933, 19948, 19950, 19961, 19964, 19966, 20016, 20020, 20040, 20041, 20051, 20067, 20078–20080, 20085, 20256, 20291, 20511, 20608, 20617, 20608, 20617, 20620, 20627, 20639, 20651, 20652, 20764, 20765, 20770, 20774, 20779, 20786, 20790, 20792, 20810, 20815, 20817, 20865, 20867, 20869, 20884, 21006, 21247, 21251, 21261, 21262, 21269, 21274, 21275, 21278, 21280–21282, 21295, 21308, 21327, 21335, 21337, 21339, 21346, 21363, 21366, 21381, 21424, 21425, 21483, 21485, 23949 (in part), and YPM-PU field number 2–72; *Plesiadapis churchilli* zone: UM 63277, 77038, 77267, 77269, 80584, 83215, 83217, 83238, 83270, 85271, 85402, 85409, 85415, 85814, 85914, 85926, 86246, 91322, 91328, 91333, 91334, 92260, 92262, 92268, YPM-PU 14967–14969, 17738, 17756, 17757, 17759, 19132, 19134, 20398, and 20399, Tiffanian: YPM-PU 19150. Wind River Basin, *Plesiadapis rex* zone: AMNH 57249, 88259, 89688, and 97040.

Ectocion mediotuber, new species
Fig. 11

Ectocion ralstonensis, Gazin, 1956c, p. 10, pl. 2:1–2.
Ectocion osbornianus, Krishtalka, 1973, p. 43, fig. 21.
Ectocion osbornianus (in part), West, 1976, p. 50, fig. 33A-B.
Ectocion osbornianum (in part), West, 1971, p. 24, fig. 18A-B.
Ectocion osbornianum, Krishtalka et al., 1975, p. 208.
Phenacodus cf. *primaevus*, Krishtalka et al., 1975, p. 109.
Phenacodus sp. (in part), Krishtalka et al., 1975, p. 209, fig. 34.
Ectocion sp. cf. *E. wyomingensis* (in part), Winterfeld, 1982, p. 100.

Holotype.—YPM-PU 17718, left dentary with P_2 to M_3 from Princeton Quarry in the Clarks Fork Basin (Sec. 21, T57N, R100W), *Plesiadapis simonsi* zone.

Age and distribution.—*Plesiadapis churchilli* and *P. simonsi* zones of the Tiffanian of the Williston, Bighorn, Wind River, Green River, Bison, and Washakie Basins.

Diagnosis.—Larger than *E. cedrus*, comparable in size
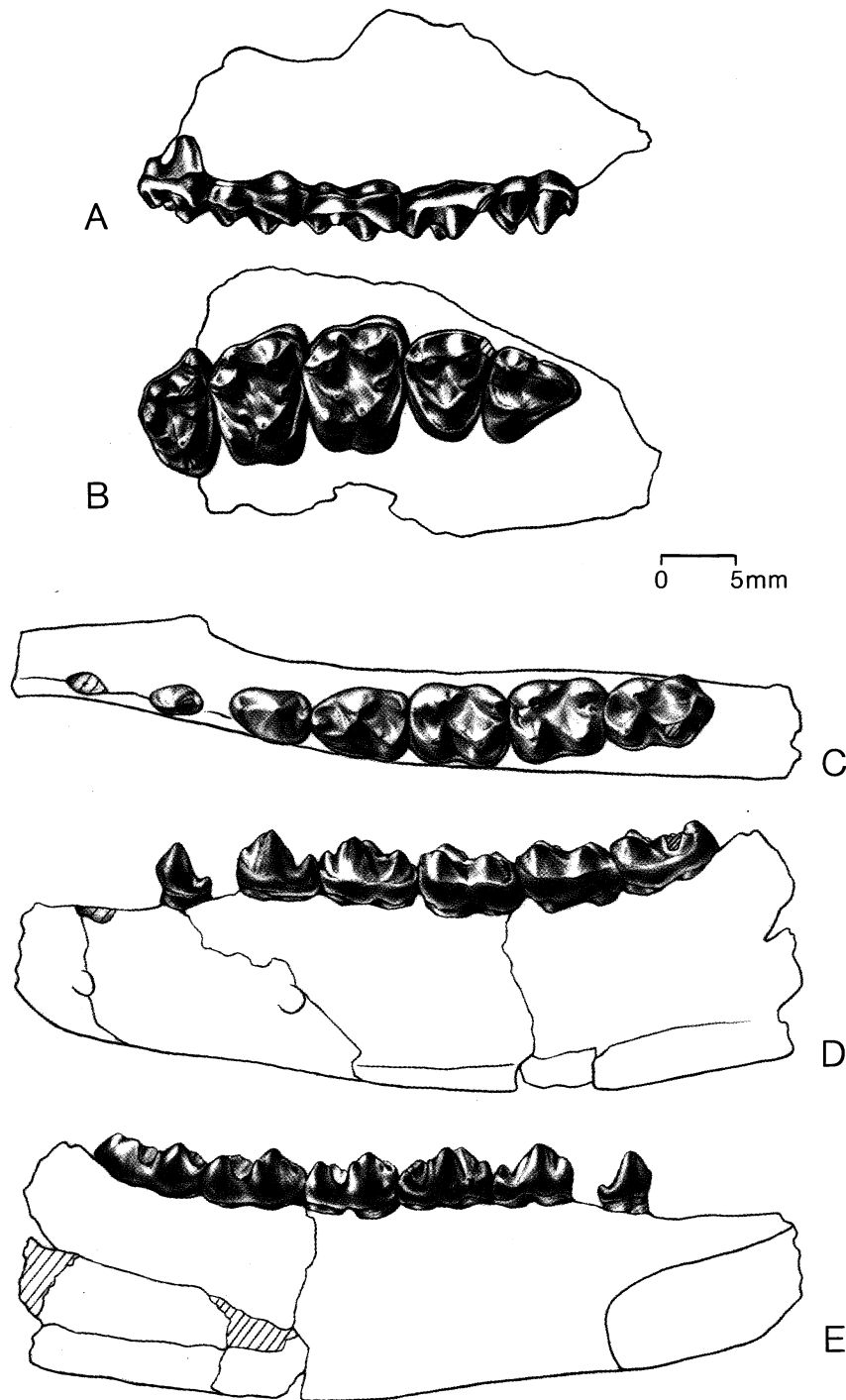
Figure 11. Dentition of *Ectocion mediotuber*. A and B, P³-M³ (YPM-PU 14532), from Clarks Fork Basin in labial and occlusal view. C through E, P₂-M₃ (YPM-PU 17718), holotype from Clarks Fork Basin in occlusal, labial, and lingual view.

to *E. osbornianus*. P$_3$ metaconid often present unlike *E. collinus*. P$_3$ hypoconid large unlike *E. collinus* and *E. cedrus*, but weaker than *E. osbornianus*. P$_3$ relatively larger than *E. cedrus* but smaller than *E. osbornianus*. P^4 paracone and metacone distant, unlike *E. collinus*.

Description.—Ectocion mediotuber is the oldest *Ectocion* for which more than the cheek teeth are adequately known. YPM-PU 18958 includes a premaxilla with the roots of the upper incisors. Judging from these roots, the crowns of the incisors decrease in size from I^1 to I^3, as in *E. osbornianus* (see there). The specimen also includes fragments of fore- and hind limb. Gazin (1956c) described a partial skull of *E. mediotuber* from the locality Buckman Hollow in the Green River Basin (USNM 20736).

The morphology of P$_3$ is the main difference between *E. mediotuber* and other *Ectocion*. The tooth is in some respects intermediate between the P$_3$ of *E. collinus* and *E. osbornianus*. It is larger than in *E. cedrus* and similar in length and width to *E. osbornianus* (Figs. 12–17), but protoconid and hypoconid are smaller than in *E. osbornianus*. Compared to the lengths of P$_4$ and M$_1$, P$_3$ is longer than in *E. cedrus* and shorter than in *E. osbornianus* (Table 2). The metaconid of P$_3$ can be present or absent. The paraconid of P$_3$ is usually low and the labial cingulum present. The paraconid of P$_4$ is usually present and smaller than in *E. cedrus*, but it is sometimes completely absent (e.g., YMP-PU 13946 and 16231). The talonid of P$_4$ is often wider than the trigonid, and the distance between protoconid and metaconid is small. The P$_4$ entoconid is present in 67% of the specimens (N = 20). The mandibular symphysis is unfused.

Discussion.—Ectocion mediotuber is similar to *E. osbornianus* in many respects and has usually been identified as such. Differences in teeth that are less often found, such as P$_3$, are hard to evaluate on the basis of small samples, and only the large collections available now make it possible to distinguish these two taxa. UM 73666 from the 680 m level of the Clarks Fork Basin section has a short P^4, resembling *E. cedrus*. In shape this tooth agrees with *E. mediotuber*: paracone and metacone are widely separated. UM 73695 from the Clarks Fork Basin has an atypical talonid with five instead of the usual three cusps.

An isolated *Ectocion* lower molar (UM 71188) from the 755 m level of the Clarks Fork Basin section is well outside the size range and more than four standard deviation units larger than the means for length and width measures of M$_1$ and M$_2$ of *E. mediotuber*. This specimen is smaller than Clarkforkian *E. major*, and is tentatively referred to *E. mediotuber*.

The largest sample of *E. mediotuber* comes from the floodplain deposits of *Plesiadapis simonsi* zone between 520 and 940 m in the Clarks Fork Basin section. A few specimens from the *Plesiadapis churchilli* zone of the Clarks Fork Basin are referred to *E. mediotuber* on the basis of size. No diagnostic premolars are preserved in this sample. The size of most of these specimens is closer to the
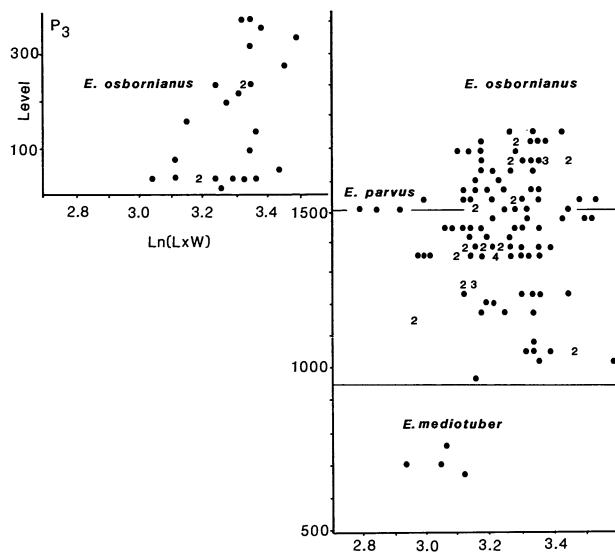
Figure 12. Scatter diagrams of natural logarithm of product of length and width (in mm) of P$_3$ for Bighorn Basin *Ectocion mediotuber, E. osbornianus,* and *E. parvus*. Ordinate is level (in meters) in central Bighorn Basin section (left) and Clarks Fork Basin section (right). Horizontal lines are boundaries between Tiffanian, Clarkforkian, and Wasatchian land-mammal ages.
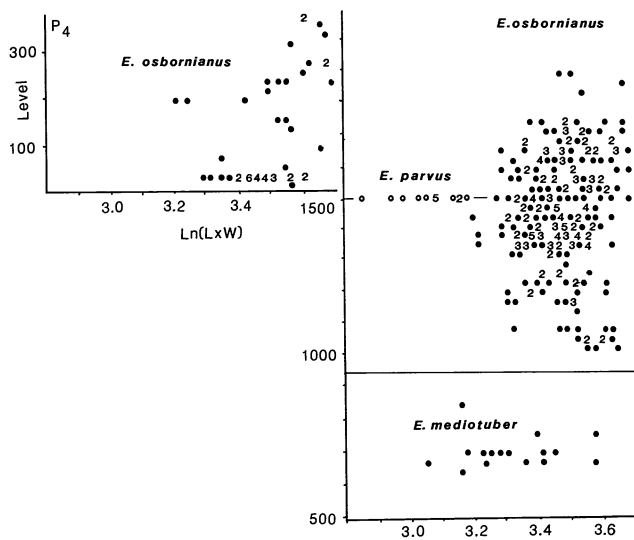
Figure 13. Scatter diagrams of natural logarithm of product of length and width (in mm) of P$_4$ for Bighorn Basin *Ectocion mediotuber, E. osbornianus,* and *E. parvus*. Ordinate is level (in meters) in central Bighorn Basin section (left) and Clarks Fork Basin section (right). Horizontal lines are boundaries between Tiffanian, Clarkforkian, and Wasatchian land-mammal ages.

mode of *E. mediotuber*, and a lower molar from Seaboard Well (YPM-PU 20406) is outside of the size range of *E. cedrus*.
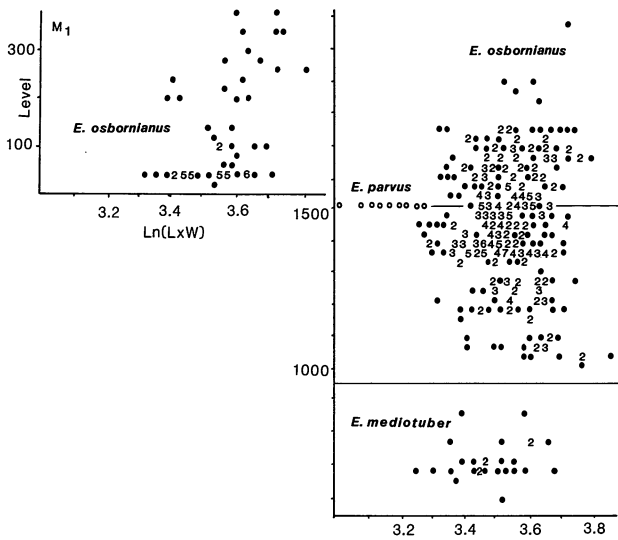
Figure 14. Scatter diagrams of natural logarithm of product of length and width (in mm) of M₁ for Bighorn Basin *Ectocion mediotuber*, *E. osbornianus*, and *E. parvus*. Ordinate is level (in meters) in central Bighorn Basin section (left) and Clarks Fork Basin section (right). Horizontal lines are boundaries between Tiffanian, Clarkforkian, and Wasatchian land-mammal ages.
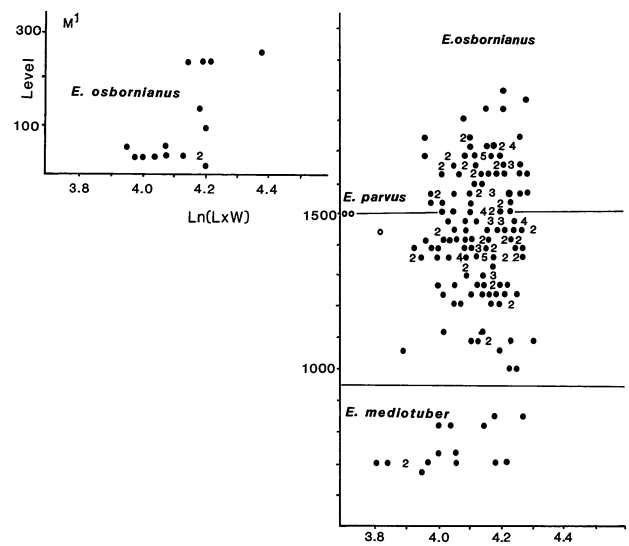
Figure 16. Scatter diagrams of natural logarithm of product of length and width (in mm) of M¹ for Bighorn Basin *Ectocion mediotuber*, *E. osbornianus*, and *E. parvus*. Ordinate is level (in meters) in central Bighorn Basin section (left) and Clarks Fork Basin section (right). Horizontal lines are boundaries between Tiffanian, Clarkforkian, and Wasatchian land-mammal ages.
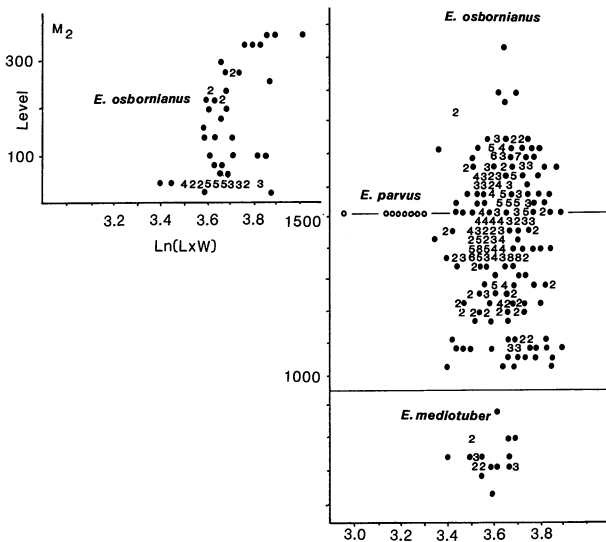
Figure 15. Scatter diagrams of natural logarithm of product of length and width (in mm) of M₂ for Bighorn Basin *Ectocion mediotuber*, *E. osbornianus*, and *E. parvus*. Ordinate is level (in meters) in central Bighorn Basin section (left) and Clarks Fork Basin section (right). Horizontal lines are boundaries between Tiffanian, Clarkforkian, and Wasatchian land-mammal ages.
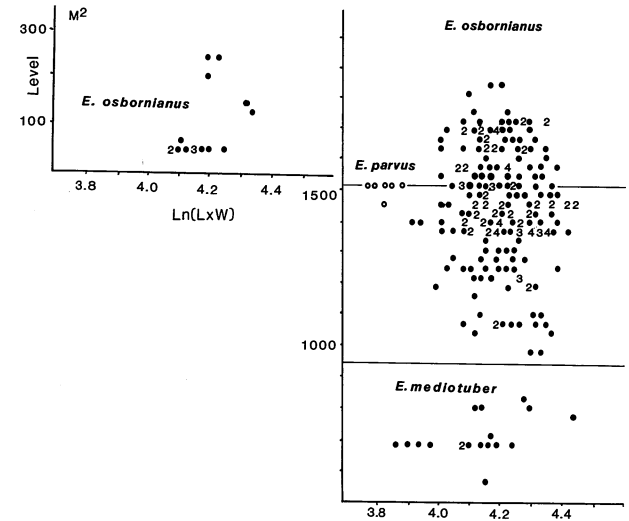
Figure 17. Scatter diagrams of natural logarithm of product of length and width (in mm) of M² for Bighorn Basin *Ectocion mediotuber*, *E. osbornianus*, and *E. parvus*. Ordinate is level (in meters) in central Bighorn Basin section (left) and Clarks Fork Basin section (right). Horizontal lines are boundaries between Tiffanian, Clarkforkian, and Wasatchian land-mammal ages.

Krishtalka (1973) referred an *Ectocion* D⁴ from Police Point in the Williston Basin (UA 5896) to *E. osbornianus*. It is not possible to differentiate between D⁴ of *E. osbornia-* *nus* and *E. mediotuber* and definite identification cannot take place until more material becomes available. The age of the fauna in which the specimen occurs is late Tiffanian,

and I therefore refer the specimen to *E. mediotuber*. Krishtalka et al. (1975) described *Ectocion* from Malcolm's locality in the Wind River Basin. These specimens are morphologically similar to *E. mediotuber*.

Only one specimen (USNM 20736) from a large collection of *Ectocion* from Buckman Hollow can be identified positively as *E. mediotuber* on the basis of its lower premolars. Other specimens lack diagnostic teeth and I therefore follow previous authors in referring other *Ectocion* from Buckman Hollow to *E. osbornianus*. Winterfeld (1982) referred late Tiffanian *Ectocion* from the Washakie Basin to *Ectocion* sp. cf. *E. wyomingensis*. These specimens are larger than average Bighorn Basin *Ectocion mediotuber*, but they are best considered *E. mediotuber* at present.

Etymology.—*Mediotuber*, from *medius* (Latin: central, midmost), and *tuber* (Latin: bump, cusp). Named for its main difference with *E. collinus* and *E. osbornianus*, the intermediate size of the hypoconulid of P_3.

Referred specimens.—Williston Basin, Tiffanian: UA 5896. Bighorn Basin, *Plesiadapis churchilli* zone: UM 71320, 71704, 71737, 83110, YPM-PU 17813, 20406, and 23688; *Plesiadapis simonsi* zone: UM 66215, 66216, 67565, 68788, 68854, 69243, 69250, 71188, 71321, 71322, 71325, 71327, 71711, 73508, 73574, 73581, 73657, 73664, 73666, 73668, 73674, 73676, 73683, 73692, 73695, 73699–73702, 73984, 74036, 79865, 79880, 80359, 85239, 91039, YPM-PU 13938, 13944–13946, 13956, 14247, 14314, 14511, 14532, 16231, 17717, 17891, 17919, 17921, 17956, 17985, 18330, 18759, 18790, 18958, 18964, 18965, 19008, 19052, 19084, 19086, 19112, 19113, 19123, 19135, 19142, 19144, 19514, 20276–20278, 20305, 20307, 20310, 20323, 20403, 20407, 20413–20416, 23695 (in part), and 23698; Tiffanian: UM 74033 and YPM-PU 18770. Wind River Basin, *Plesiadapis churchilli* zone: CM 16195, 16196, 16209, 16211, 16213, 16215, 23768, 23769, 23778–23781, and 23783. Green River Basin, Tiffanian: USNM 20736. Bison Basin, *Plesiadapis simonsi* zone: USNM 405063, UW 1080, and 1092. Washakie Basin, *Plesiadapis churchilli* zone: UW 10495, 13239, 13242, 13244–13248, and 15245; *Plesiadapis simonsi* zone: UW 10499 and 10574.

Ectocion osbornianus (Cope, 1882a)
Figs. 18 and 19

Oligotomus osbornianus Cope, 1882a, p. 182.
Ectocion osbornianum, Cope, 1885, p. 696, pl. 25f:9–10; Granger, 1915, p. 352, fig. 11B and 12B; Davidson, 1987, p. 115.
Ectocion ralstonensis Granger, 1915, p. 353, fig. 11B, 12B, and 14.
Ectocion osbornianus ralstonensis, Simpson, 1937c, p. 19.
Ectocion sp., Gazin, 1942, p. 220.
Ectocion osbornianus complens Simpson, 1943, p. 174.
Ectocion cf. *osbornianum*, Gazin, 1956c, p. 13.
Ectocion osbornianus?, McKenna, 1960, p. 101, fig. 55.
Ectocion osbornianus (in part), Delson, 1971, p. 346; Rose, 1981, p. 73, fig. 32.
Ectocion osbornianum (in part) West, 1971, p. 24, fig. 18C; West, 1976, p. 50, fig. 33C-D, 34–36, and 37B.
Ectocion cf. *osbornianus*, Bown, 1979, p. 99, fig. 55d and 56a-c; Gingerich, 1989, p. 52.

Holotype.—AMNH 4409, dentary and maxilla fragments with left P_3 fragment, P_4-M_2, P^3 fragment, P^4-M^2, and right M_2, P^4, and M^1 fragment. The specimen was collected by "Mr. J. L. Wortman in the bad lands of the Big-Horn River" (Cope, 1882a:183). Granger (1915:352)

states that the specimen comes from the "Gray Bull beds" of the Bighorn Basin.

Age and distribution.—*Plesiadapis gingerichi* zone of the Clarkforkian through Upper *Haplomylus-Ectocion* zone of the Wasatchian of the Powder River, Bighorn, Wind River, Green River, Washakie, Sand Wash, Laramie, and Piceance Basins.

Diagnosis.—Large *Ectocion*, size comparable to *E. mediotuber*, larger than *E. parvus*, but smaller than *E. major* and *E. superstes*. P_3 large, metaconid weak or absent, and large protoconid and hypoconid unlike *E. collinus*, *E. cedrus* and *E. mediotuber*. P_4 with wide trigonid basin unlike *E. mediotuber*. P^4 paracone and metacone well separated unlike *E. collinus*.

Description.—All permanent teeth as well as D^{2-4}, and D_{2-4} are known for *E. osbornianus*. West (1971) described the deciduous dentition. A Clarkforkian skull of *Ectocion osbornianus* is described in Chapter V (UM 86155).

Specimens in which the adult dentition is well preserved include UM 57702, 57703, 73356, 86155, and YPM-PU 16231. The upper incisors are worn in all available I^{1-2}, but their tips were apparently originally pointed. I^3 has a pointed tip and is separated from I^2 and C^1 by a short diastema. The upper canine is curved and mediolaterally flat, the surface has faint longitudinal ridges. The maxilla is pitted anterior to the upper canine to house the tip of the lower canine. P^1 and P^2 are double rooted, P^1 is shorter and higher crowned than P^2. P^2 has a weak cingulum. Diastemata separate C^1, P^1, and P^2. The lower incisors are spatulate (UM 73356, YPM-PU 16231), and probably not separated by diastemata in life. A small diastema is present between I_3 and C_1. The lower canine is rounded in cross section and more slender than C^1, but shows similar longitudinal ridges. P_1 is single rooted and pointed. P_2 is double rooted and comparable in size but less wide than P^2. Diastemata occur between C_1, P_1, and P_2. P_2 has a higher crown than P^2. The parastyle of P^3 is large. P_3 is enlarged with an inflated protoconid and hypoconid, and the metaconid is often absent. The trigonid basin of P_4 is wide and usually lacks the paraconid. *Ectocion osbornianus* is comparable in size to *E. mediotuber* (Figs. 12–17) and is best distinguished from it and other Tiffanian *Ectocion* on the basis of P_3 (see discussion of *E. mediotuber*). West's (1976) claim that premolars of *E. osbornianus* are more molarized than those of Tiffanian taxa is not apparent. *E. osbornianus* is morphologically similar to *E. parvus*, but differs in size (Gingerich, 1989).

Discussion.—"*E. osbornianus*" is sometimes spelled as "*E. osbornianum*." Cope (1882a) proposed the name *Oligotomus osbornianus* for the holotype, and referred it to a new genus later: *Ectocion* Cope, 1882c. Cope never discussed the etymology, but the latter name is apparently composed of the latinized Greek "ekto" (outward) and "kioon" (column). Cope (1885) implied that *Ectocion* is neuter, citing "*Ectocion osbornianum*." This is incorrect, the Greek "kioon" can be masculine or feminine and should
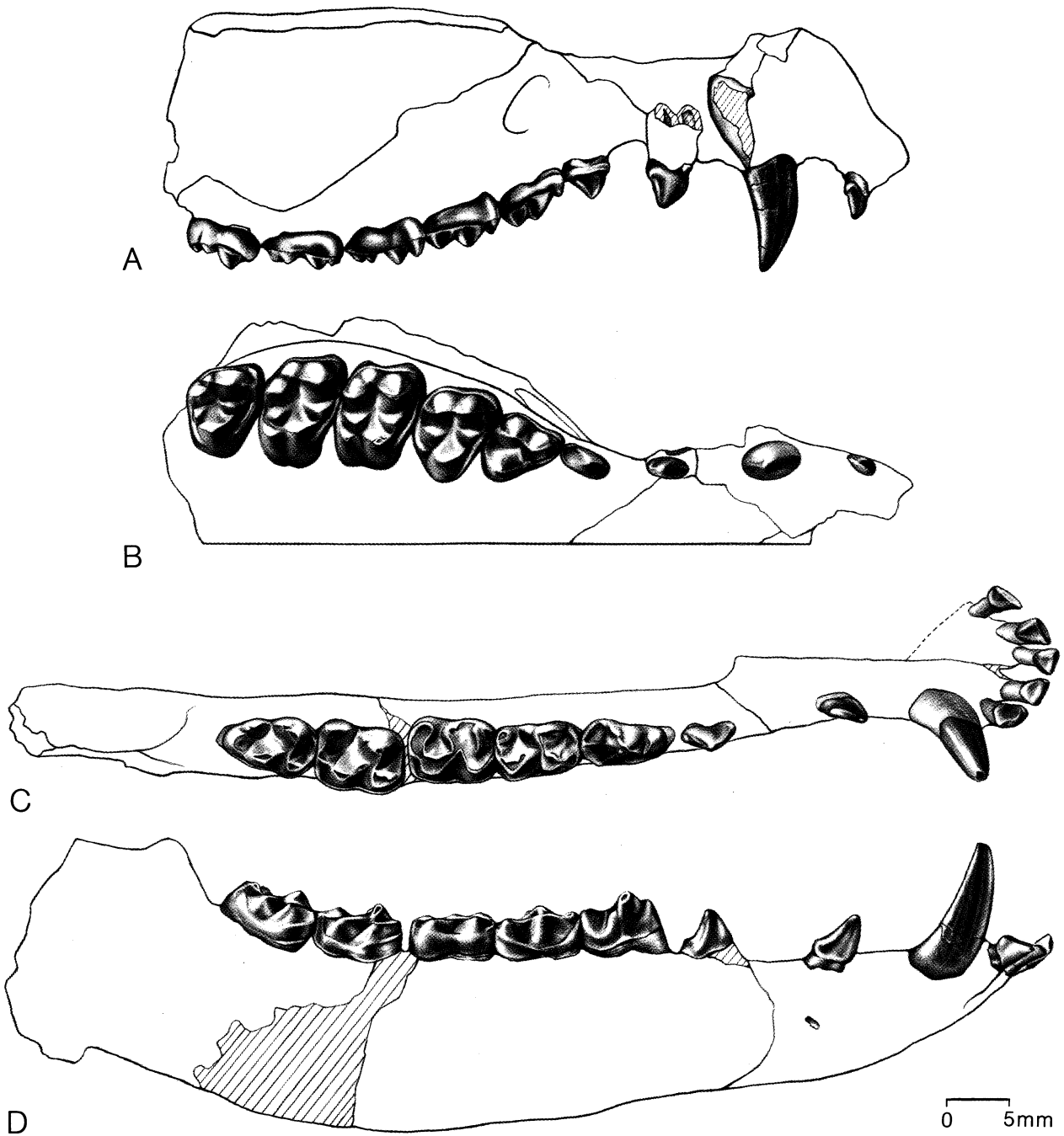
Figure 18. Dentition of *Ectocion osbornianus*. A and B, I^3-M^3 (UM 57702) from middle Clarkforkian of Krause Quarry, labial and occlusal view. C and D, left I_{1-3} and right I_2-M_3 (UM 73356) from Clarks Fork Basin, occlusal and labial view. Judging from canine size the specimen is female (compare with male of fig. 55).

be interpreted as masculine for use in zoological names according to the Code of Zoological Nomenclature. The adjective also assumes this gender, ending with -us. Cope (1887) used a latinized neuter form of "*Ectocion*," citing

"*Ectocium*." This is clearly a *lapsus calami* and should not be used. The trigonid of P_4 of the holotype is shorter than in most referred *E. osbornianus*.

Ectocion osbornianus is the most abundant phenacodon-
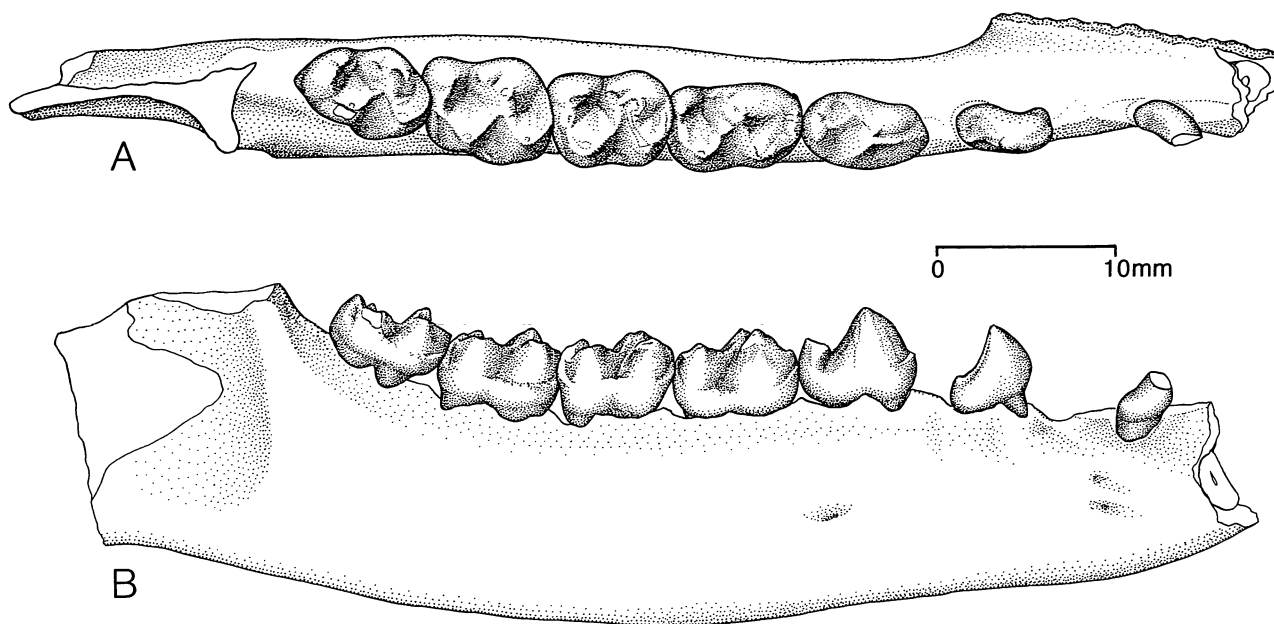
Figure 19. Dentition of *Ectocion osbornianus*. A and B, P₁-M₃ (UM 71804), early Clarkforkian of Clarks Fork Basin, occlusal and labial view. Reprinted from Rose (1981), drawing by Karen Klitz.

tid, and one of the most common mammals of the Clarkforkian (Rose, 1981). Granger (1915) distinguished two Clarkforkian and Wasatchian taxa: larger *Ectocion osbornianus* and smaller *E. ralstonensis*. Simpson (1937c) considered these to be extremes of a chronocline, and gave them subspecific status. In 1943, Simpson included the holotype of *E. parvus* in *E. osbornianus ralstonensis*, and divided the chronocline into four subspecies, *E. osbornianus ralstonensis, E. osbornianus complens, E. osbornianus osbornianus,* and *E. osbornianus superstes*. In Simpson's view, there was size increase in this chronocline, but actual subspecific boundaries were determined by the age of the specimen. McKenna (1960) pointed out that *E. parvus* and *E. superstes* were probably valid species, and Delson (1971) suggested that the two remaining subspecies were invalid, and that the stratigraphic framework used by Simpson might be inaccurate. Rose (1981) documented the latter statement, and Gingerich (1985) demonstrated that there is no consistent size change in M₁ in *E. osbornianus* from Clarkforkian to early Wasatchian. I retain *E. parvus* and *E. superstes,* but synonymize *E. ralstonensis* and *E. o. complens* with *E. osbornianus*. No size change is apparent in the lineage (Figs. 12–17).

Ectocion osbornianus co-occurs for part of its stratigraphic range with another phenacodontid of similar size, *Copecion brachypternus*. Compared to *Copecion, Ectocion* has a larger width/length ratio for P³, P⁴, M² (Table 3). P₃ often bears a paraconid and always a hypoconid in *Ectocion*

Table 3. Ratios of cheekteeth dimensions of *Ectocion osbornianus* and *Copecion brachypternus*.

	E. osbornianus			C. brachypternus		
	N	Mean	SD	N	Mean	SD
P³W/L	99	1.00	0.08	8	0.80	0.08
P⁴W/L	149	1.18	0.08	15	1.11	0.07
M²W/L	10	1.47	0.09	10	1.36	0.07
P₄W/L	379	1.43	0.10	60	1.63	0.11
P₄L/M₁L	232	1.03	0.07	36	1.15	0.07

osbornianus, whereas these cusps are always absent in *Copecion*. The trigonid of P₄ is more elongate in *Copecion* than in *Ectocion*. Only 6% of available P₄s of *Copecion brachypternus* have an entoconid (N = 63), whereas 64% of *Ectocion osbornianus* have this cusp (N = 376). *Ectocion* also has more lophodont molars, with a deeper trigonid basin. The paracristid of *Ectocion osbornianus* descends to the base of the crown in 90% of the M₂s (N = 568), and ascends the metaconid in 92% of *Copecion brachypternus* (N = 78). M₃ usually has a pronounced notch between hypoconulid and entoconid in *Copecion,* whereas these cusps are connected by a crest in *Ectocion*. The mesostyle of the upper molars is larger in *Ectocion* than in *Copecion* (p<.005).

YPM-PU 16231 is a problematic phenacodontid speci-

men. It consists of remains of at least four phenacodontids: a palate of *Ectocion* with two dentaries lacking only upper and lower right incisors (see Fig. 34 of West, 1976); two maxillae and dentaries of *Ectocion* with left and right P^3-M^3, left P_3-M_3, and right P_3-M_2; an *Ectocion* dentary with M_1-M_3; and a *Phenacodus* dentary with P_2-P_3. According to the label the specimen was collected "S. of Fossil Hollow," but later more specific locality information was added in different ink: "SW 1/4, S25, T57N, R100W, Park Co., Wyo." The outcrops in this quadrant yield a fauna from the *Plesiadapis simonsi* zone, but the morphology of the P_3's of *Ectocion* of YPM-PU 16231 is clearly that of *E. osbornianus*. I assume that the locality information added to the label was wrong, and that these specimens were in fact collected a mile or more south of Section 25, in Clarkforkian beds.

A teratological phenacodontid from the Lower *Haplomylus-Ectocion* zone was described by Rose and Smith (1979), who referred it to *E. osbornianus* (UM 69450). P_3 and P_4 on both sides of the specimen are equally aberrant, and no similar specimens have been recovered since its description. In a middle Clarkforkian specimen (UM 73356), P_2 and its alveoli are missing in the left dentary, but present in the right dentary. The mandibular symphysis of one middle Clarkforkian *Ectocion* specimen (UM 86255) is fused, unlike other specimens.

West (1976) and Rose (1981) have suggested that variation in synchronous samples of *E. osbornianus* is larger than usual for monospecific taxa. I observed no bimodality in any character. Coefficients of variation exceed 10 for approximately 20% of the quantified variables in late Clarkforkian and early Wasatchian *Ectocion osbornianus*. The largest coefficients of variation occur in the measures that have high coefficients in other phenacodontids as well, such as the height of the mesostyle. Fig. 20 shows the variability of lower molar dimensions in nearly a hundred samples of *Ectocion osbornianus* as a function of sample size. Variability is expressed as the standard deviation of the natural logarithm of the product of length and width in M_1 and M_2. The standard deviations converge on values near .10 at higher sample sizes. These values are similar to those in other mammals (Gingerich and Winkler, 1979; Gingerich, 1985).

I tested the normality of distributions for two levels with the largest samples of *Ectocion* from the Clarks Fork Basin section, using a modified version of the Kolmogorov-Smirnov test (Lilliefors, 1967). The tested levels are middle Clarkforkian 1370 m (N = 100) and early Wasatchian 1665 m (N = 74). For the 1370 m level eight out of 21 tested variables were significantly different from normal and for the 1665 m level two out of 21. I believe that the smaller number of deviations at the Wasatchian level is due to lower sample size and not to inhomogeneity of the sample. Within these samples, the large number of specimens with missing data often result in sample sizes of individual variables of less than 10, leading to a decrease of the power
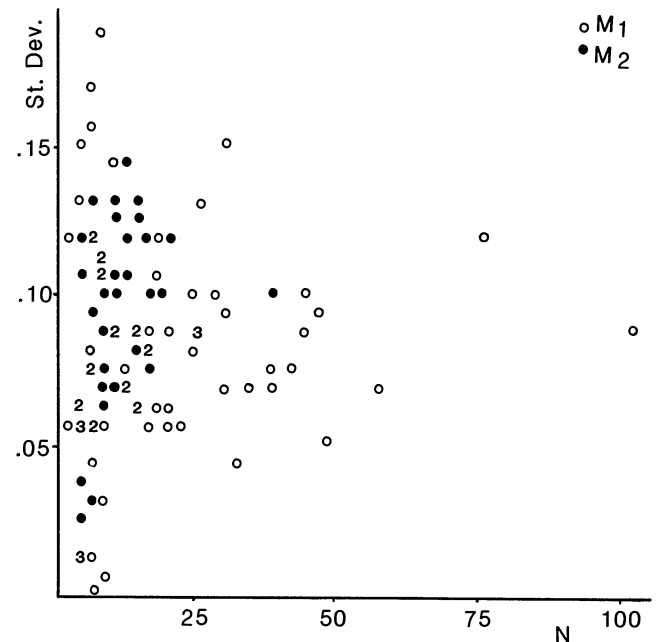
Figure 20. Scatter diagram of standard deviation of natural logarithm of product of length and width (in mm) of M_1 and M_2 versus sample size. Samples are *Ectocion osbornianus* from single levels in Clarks Fork and central Bighorn Basin sections.

of the test. In those cases the conservative H_0 of normality is accepted.

Ectocion osbornianus possibly increases in size from the Lower to Upper *Haplomylus-Ectocion* zone (Figs. 12–17). Evolution in shape occurs throughout the range of *E. osbornianus*. The frequency of the incidence of an entoconid on P_4 decreases: in the *Plesiadapis gingerichi* and *P. cookei* zone this cusp is common, as in Tiffanian *E. mediotuber* (77% and 67% respectively, N = 13 and 94), but in late Clarkforkian and Wasatchian samples the cusp is often absent (41% and 52% respectively, N = 58 and 111). The incidence of a metaconid on P_3 also decreases: in Clarkforkian *E. osbornianus* the cusp is absent in 30% of unworn specimens (N = 27), and in Wasatchian specimens it is absent in 76% (N = 37).

Present evidence suggests, but does not prove, that *Ectocion osbornianus* was sexually dimorphic. Bimodality occurs in the height of the canines but not in their lengths (Fig. 21). Sexual dimorphism may also be present in the skull (see Chapter V). Possible sexual dimorphism in *Ectocion* was previously investigated by Gingerich (1981), who concluded that *Ectocion* was not dimorphic or not dimorphic to the extent that *Hyracotherium* is.

Although most teeth of *Ectocion osbornianus* are sufficiently different for unambiguous determination of their place in the tooth row, this is not true for M_1 and M_2. Rose (1981) investigated a similar problem for Clarkforkian
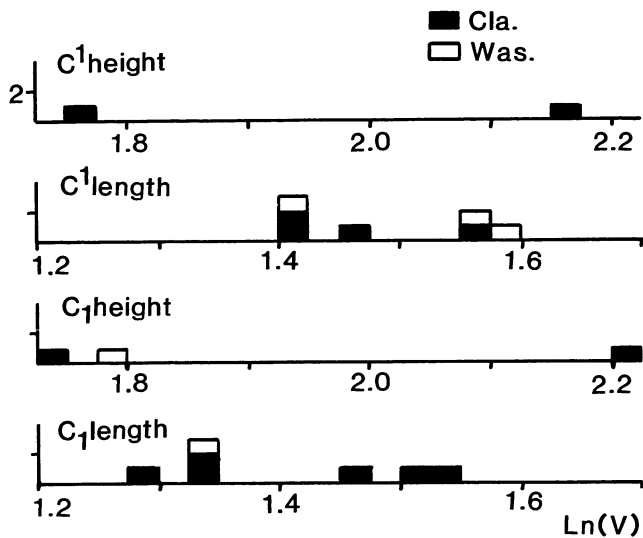
Figure 21. Histogram of natural logarithm of length and height (in mm) of C_1 and C^1 (Ln [V]) in Clarkforkian and Wasatchian *Ectocion osbornianus*. Sexual dimorphism is apparent in canine height.

Phenacodus, and calculated indices of length and width in order to determine if isolated molars were M_1 or M_2. Rose found that his indices were not consistently different for the two teeth.

In an attempt to distinguish between isolated M_1 and M_2 in *Ectocion osbornianus*, I used discriminant function analysis. The first canonical discriminant function was derived from five measures of *Ectocion osbornianus* M_1 and M_2 in which determination was unambiguous. The five measures for each tooth were: length, width of trigonid, width of talonid, length of trigonid basin, and width of trigonid basin. The centroids of the two samples of 109 M_1s and 186 M_2s were significantly different and the first canonical discriminant function is: 0.155(length) + 3.85(trigonid width) - 3.06(talonid width) + 0.66(trigonid basin length) + 1.00(trigonid basin width). A histogram of the scores for this function for 295 molars in the analysis is presented in Fig. 22. In order to evaluate the usefulness of the function in classifying molars for which the position in the jaw is not known, I used it to classify the molars on which the analysis was based. The function classified 24% of true M_1s as M_2, and 34% of true M_2s as M_1. A probability can be calculated for the score of each specimen, indicating how likely classification in one group is (posterior probability). Fig. 22 also presents a histogram of the posterior probability of being classified as M_1 for the molars for which the position is known. Although true M_2s have a low probability of being classified as M_1, the region of overlap of the distributions is large, and classification of unknown molars is not effective.

E. osbornianus is found between 990 m and 2095 m, near the top of the Clarks Fork Basin Section (*Plesiadapis*
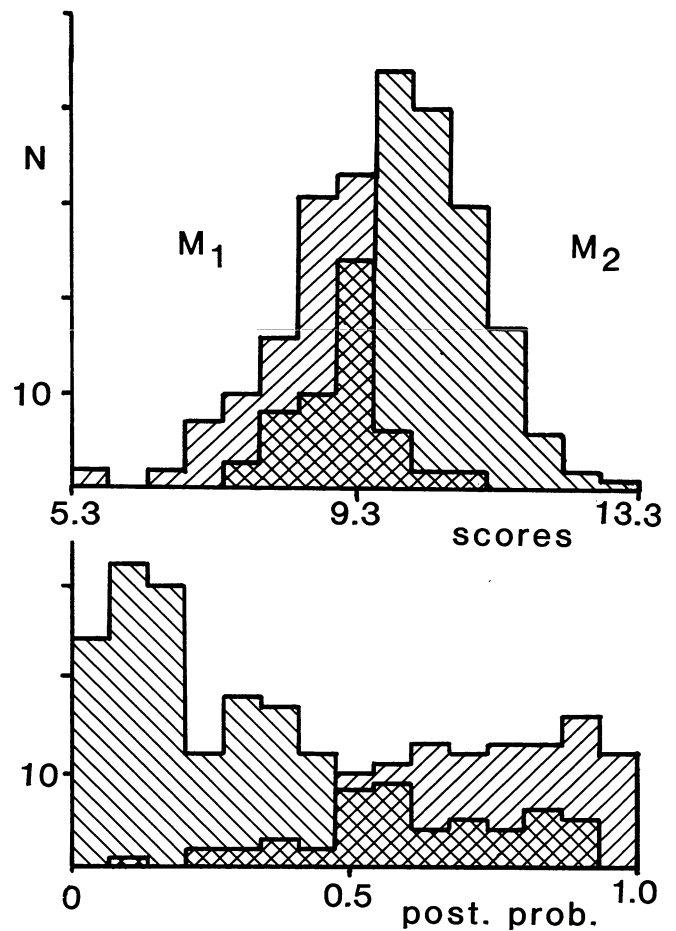
Figure 22. Histogram of results of discriminant function analysis of 295 pairs of associated M_{1-2}s of *Ectocion osbornianus*. Top diagram displays scores of specimens on first canonical discriminant function listed in text. Bottom diagram displays probability of known specimen of being classified as M_1 by the function (posterior probability). Cross hatching identifies specimens as M_1 and M_2.

gingerichi through Upper *Haplomylus-Ectocion* zones). The last specimens occur at 379 m in the central Bighorn Basin Section (Upper *Haplomylus-Ectocion* zone).

Ectocion osbornianus has been described from several Wasatchian localities in the Powder River Basin (Delson, 1971).

Ectocion osbornianus has been found at locality 13E (Keefer, 1965) in the Indian Meadows Formation of the Wind River Basin. The occurrence of *Ectocion* with *Phenacodus trilobatus* and *P. intermedius* is consistent with the interpretation of the age of this fauna: the Upper *Haplomylus-Ectocion* zone. *E. osbornianus* is also known from a number of Clarkforkian localities in the Togwotee Pass area. A P_3 from Robinson's Taeniodont locality (AMNH 86851) matches early Clarkforkian *Ectocion osbornianus*

from the Bighorn Basin more closely in size than middle Clarkforkian *E. osbornianus*. Mean P_3 size of the *P. cookei* zone is smaller than in the *P. gingerichi* zone, although the size difference is not significant. If the apparent pattern is corroborated by more finds, it would suggest that the Togwotee Pass localities at this level yield faunas from the *Plesiadapis gingerichi* zone. This is consistent with interpretation of the local stratigraphy.

A collection of *Ectocion* from Buckman Hollow (Gazin, 1942, 1956c; Dorr and Gingerich, 1980) is here referred to *E. osbornianus*, on the basis of the generally accepted age for this fauna (Rose, 1981). One *Ectocion* specimen can be positively identified as *Ectocion mediotuber* on the basis of its P_3 (see discussion for this taxon).

One specimen of Clarkforkian *Ectocion osbornianus* is known from Bitter Creek Road 1 (UCMP 111878) and several are known from Big Multi Quarry in the Washakie Basin. Wasatchian specimens are known from the Four Mile Fauna of the Sand Wash Basin (McKenna, 1960) and from the Cooper Creek Fauna in the Laramie Basin (Davidson, 1987). The taxon is less abundant at these southern localities than at sites of similar age from the Bighorn Basin.

Referred specimens.—Powder River Basin, Wasatchian: AMNH 56159–56161, 56304, 93271, 93272, 93274, and 93275. Bighorn Basin, *Plesiadapis gingerichi* zone: UM 85247, 85248, YPM-PU 18306, 18928, 18934, 18936, 18945, 18951, 18988, 18991, 19828, 20266, UM 66197, 68026, 68031, 68410, 68412, 68413, 68415, 68418, 68422, 68424, 68425, 68427, 68433, 68435, 68749, 68751, 68752, 68757, 68891, 69921, 69922; 69924, 69926, 69927, 71262, 71296, 71298, 71308, 71314, 71315, 71358, 71372, 71613, 71616–71618, 71621, 71622, 71625, 71626, 71773, 71777, 71804, 71806, 71814, 71815, 71818, 73335, 73341, 73359, 73362, 73373, 73374, 73525, 73705, 73715, 73718, 73723, 83162, and 83164; *Plesiadapis cookei* zone: UM 57087, 57697–57699, 57702, 57703, 64992, 64993, 64995–64997, 65005, 65007, 65012, 65017–65019, 65021–65023, 65025–65027, 65029, 65030, 65032, 65034, 65052, 65058, 65235–65237, 65242, 65243, 65246, 65248, 65250–65253, 65257, 65259, 65260, 65474, 65475, 65477, 65479, 65486, 65488, 65489, 65523–65526, 65532, 65535–65537, 65539, 65541, 65543, 65544, 65548, 65549, 65553, 65557, 65558, 65633, 65638, 65639, 65641, 65643, 65646, 65647, 65664, 65717–65719, 65776, 65779, 65781, 65782, 66126, 66181, 66203–66207, 66323, 66324, 66328, 66329–66331, 66333, 66498–66501, 66503, 66532, 66534, 66537, 66540, 66541, 66545, 66623–66626, 66631, 66637, 66638, 66640, 66641, 66645, 66698, 66699, 66708, 66710, 66711, 66713, 66714, 66717, 66721–66724, 66726, 66729, 66733, 66738, 66743, 66744, 66745, 66748, 66750, 66756, 66760, 66762, 66766, 66767, 66770, 66906, 66907, 66916, 66917, 66920, 67020, 67025, 67027, 67028, 67181, 67182, 67185, 67192–67195, 67197, 67198, 67202, 67204–67210, 67213, 67215–67219, 67222, 67352, 67353, 67356, 67358, 67557, 68226, 68229, 68230, 68232, 68234, 68235, 68240–68243, 68246, 68247, 68286, 68508, 68510, 68512–68514, 68516, 68518–68521, 68862, 68877, 68880, 68882, 69173, 69176, 69180, 69226–69229, 69234, 69257, 69259, 69260, 69262, 69263, 69267, 69268, 29272, 69275, 69302, 69304, 69311, 69315, 69318, 69320, 69323, 69328–69330, 69346, 69443, 69444, 69669, 69675, 69676, 69679, 69688, 69692–69695, 69697, 69900, 69902–69904, 69909–69912, 69915–69919, 69935, 69936, 69997, 71051–71053, 71169, 71174, 71180, 71182, 71235, 71239, 71435–71437, 71442, 71444–71446, 71450–71452, 71454, 71456, 71461, 71462, 71470, 71472, 71486, 71488, 71494, 71633, 71640, 71647, 71648, 73356, 73409, 73413, 73416, 73573, 73874, 73888,

73996, 74039, 74052, 75445, 75670, 76130, 76763, 76848, 77558, 77560, 77563, 79488–79490, 79671, 80239, 80241, 80242, 80252, 80272, 80273, 80275, 80344–80352, 80441, 80560, 80563, 80564, 80566, 82016, 82361, 82366, 82367, 82369, 82371, 82372, 82620, 83012, 83160, 83172, 83176, 83177, 83180, 83186, 83188, 83189, 83424, 83438, 83744, 83746–83749, 83752, 83755, 83756, 83758, 85992, 86148, 86149, 86151, 86154, 86155, 86158, 86160, 86251, 86252, 86255–86257, 86264, 86266, 86267, 86270, 86271, 86561, 87796, 87797, 87805, 87807, 87808, 87811, 87812, 87828, 87980, 87997, 87998, 88000, 88002, 88005, 88174–88176, 88180, 88184–88186, YPM-PU 18086, 18095, and 18305; *Phenacodus-Ectocion* zone: UM 64707, 64710, 64712, 64715, 64717, 64719–64725, 65062, 65064, 65065, 65068, 65070, 65074, 65076, 65077, 65082, 65085, 65086, 65087, 65089–65091, 65093–65097, 65100, 65103, 65105, 65107–65111, 65113–65116, 65126, 65128, 65472, 65518, 65520, 65651, 65652, 65655, 65669, 65670, 65673–65677, 66111, 66168, 66170, 66172, 66190–66192, 66293, 66296, 66299, 66303, 66306, 66308, 66311, 66314, 66315, 66573, 66575–66577, 66579–66581, 66590, 66596, 66601, 66619, 66620, 66846, 66849, 66851, 67224, 67225, 67228–67233, 67235, 67237–67241, 67259, 67441, 67447–67449, 67451, 67453, 67455, 67458, 67465–67467, 68034, 68038, 68203, 68207, 68218, 68234, 68781–68783, 68785, 69281–69283, 69286–69289, 69292–69294, 69347, 69873, 69875, 69878, 69879, 69881–69883, 69886–69889, 69891–69893, 69895, 69897, 71242, 71419–71422, 71425–71429, 71432, 71478, 71479, 71492, 72603, 73727, 73765, 73778, 76865, 81912, 81913 (in part), 83167, 83168, 83178, 83181, 83183, 83185, 83432, 83621, 83786, 83789, 83792, 83804, 83877–83879, 83881, 86566, 86567, 92672, 92673, 88155–88157, 91418, 91421–91426, and 91466; *Cantius torresi* zone: UM 66612 and 83875; Lower *Haplomylus-Ectocion* zone: UM 63578, 63830, 64432, 64534, 64585, 64590, 64605, 64606, 64619, 64626, 64628, 64658, 64671, 64685, 64687, 64697, 64737, 64755, 64782, 64787, 64818, 64821, 64847, 64872, 64882, 64883, 64885, 64890, 64894, 64900, 64901, 64904, 64908, 64938, 64940, 64941, 64946, 64947, 64948, 64952, 64957, 64963, 64971–64973, 64979, 64989, 65131, 65134, 65142, 65160, 65169, 65173, 65185, 65186, 65191, 65201, 65210, 65212, 65215, 65216, 65218, 65323, 65326, 65373, 65374, 65381–65384, 65400, 65414, 65421, 65423, 65436, 65439, 65444, 65497, 65504, 65508, 65587, 65608, 65617, 65628, 65630, 65695, 65700, 65706, 65713, 65771, 66228, 66342, 66343, 66348, 66354, 66355, 66359, 66367–66369, 66374, 66378, 66388, 66397, 66437, 66448, 66518, 66589, 66604, 66605, 66608, 66609, 66772, 66885, 66897, 66926, 66942, 66944, 67009, 67013, 67103, 67124, 67146, 67379, 67383, 67386, 67391, 67394, 67399, 67413, 67419, 67430, 67438, 67510, 67545, 68021, 68022, 68085, 68113, 68135, 68137, 68147, 68168, 68176, 68178, 68185, 68320, 68324, 68447, 68462, 68477, 68492, 68493, 68570, 68572, 68586, 68600, 68641, 68642, 68709, 68713, 68759, 68832, 68850, 69349, 69363, 69392, 69397, 69450, 69469, 69470, 69476, 69553, 69731, 69733, 71273, 71276, 71278, 71757, 72124, 72125, 72148, 72161, 72243, 72253, 72844, 72845, 72854, 72867, 72875, 72877, 72897, 72899, 72910, 72912, 73743, 73744, 73766, 73767, 73778, 73782, 73850, 74048, 75086, 75111, 75120, 75152, 75161, 75170, 75172, 75212, 75236, 75252, 75307, 75408, 75595, 75615, 75616, 75752, 75757, 75764, 75773, 75856, 75915, 75930, 75963, 75967, 75987, 75989, 76014, 76029, 76108, 76109, 76114, 76143, 76163, 76204, 76214, 76218, 65220, 76221, 76224, 76245, 76331, 76350, 76389, 76396, 77427, 77430–77432, 76450, 76471, 76482, 76483, 76564, 76568, 76635, 76691, 76832, 76840, 76842, 76843, 77357, 77378, 77451, 77464, 77465, 77468, 77469, 78910, 78926, 79024, 79036, 79061, 79091, 79106, 79127, 79135, 79138, 79149, 79373, 79375, 79399, 79402, 79415, 79678, 79712, 80032, 80055, 80074, 80086, 80173, 80175, 80185, 80198, 80213, 80218, 80224, 80287, 80288, 80290, 80299, 80302, 80304, 80307, 80311, 80379, 80386, 80400, 80404, 80415, 80492, 80497, 80505–80507, 80519, 80550, 80551, 80555, 80588, 80608, 80686, 80696, 80779, 80780, 80786, 81925, 81963, 82291, 81194, 82147, 82196, 82200, 82298, 82323, 82466, 82573, 82725, 82828, 83097, 83098, 83100, 83108, 83119, 83187, 83291, 83310, 83316,

83341, 83402, 83509, 83610, 83767, 83772, 83828, 83829, 85574, 85824, 85876, 85877, 85885, 85896, 85897, 85952, 86044, 86057, 86058, 86062, 86082, 86098, 86102, 86104, 86106, 86112, 86315, 86353, 86407, 86427, 86431, 86432, 86478, 86514, 86517, 86528, 86774, 86782, 87196, 87325, 87362, 87403, 87419, 87453, 87454, 87456, 87465, 87466, 87496, 87528, 87536, 87553, 87578, 87585, 87654, 87683, 87828, 87841, 87845, 87861, 88161, 88329, 90975, USGS 1917, 2604, 3570, 3600, 5040, 5042, 5046–5055, 8325, 19314, 23692, 23924, 23930, 27700, 83261, UW 7957, 9335–9337, 9339, 9343–9345, 9347, 9351, 9352, 9354, 9357, 9359, 9361, 9362, 9364, 9366, 9370, 9371, 9373, 9374, 9376, 9377, 9379, 9381–9384, 9386–9392, 9398, 9401, 9402, 9413, 9414, 9415, 9417, 9419, 9421, 9423–9429, 9433, 9434, 9438–9442, 9444–9451, 9454, 9456, 9457, 9458, 9460–9471, 9475, 10269–10274, 10328, YPM 22966, 22975, 23529, 23683–23685, 23689, 23691, 23701, 23702, 26262, 26549, 26993, 27048, 27056, 32070, 32095, 32137, 32153, 32169, 32202, 32293, 32423, 32467, 32556, 32596, 32646, 32732, 32812, 33137, 33924, 33926, 33929, 33931, 34347, 35983, 36361, 36364, 36370–36375, 36378, 36379, 36381, 36701, 41440, and 41441; Upper *Haplomylus-Ectocion* zone: UM 63757, 63804, 65317, 65348, 65353, 67171, 67288, 69631, 69974, 71198, 71218, 71223, 72832, 73050, 73084, 73793, 73821, 73946, 73950, 75284, 76796, 79163, 79241, 79313, 79341, 82838, 82842, 82869, 82890, 82980, 83026, 83063, 85684, 85746, 87019, USGS 1777, 2222, 2453, 2493, 4338, 4346, 5043–5045, 5134, 5147, 7950, 8016, 8066, 8975, 8976, 9383, 9666, 9676, 10179, 17873, 19291, YPM 21848, 22955, 22957, 25131, 25157, 25164, 25240, 25852, 25916, 25926, 26031, 26329, 26644, 27112, 31985, 32040, 32322, 32341, 32351, 32804, 32841, 32872, 34431, 34432, 34434, 34436, 36362, 36363, 36365, 36368, 36370, 36383, 36384, 36691, 36705, 41435, 41436, 41438, and YPM-PU 18301; Clarkforkian: UM 86589, 87206, 92285, YPM-PU 18975, 18976, and 20410; Clarkforkian?: AMNH 15853 (holotype *E. ralstonensis*), 16050, UM 82663, 85296, 85393, 85422, 85423, 86590, 87210, and 87260; Wasatchian: AMNH 15325, 22498 (holotype *E. osbornianus complens*), UM 63776, 82664, 85257, 85260, 85276, 85320, 85326, 85346, 85355, 85360, 85942, 87220, 90967, 91091, USGS 1676, 2211, 2212, 2602, 10182, YPM 21697, 21803, 21852, 21858, 22956, 22958, 22959, 22961, 22969, 22971, 22972, 25922, 32574, 32805, 32813, 32982, 33064, 33097, 36366, 36376, 37866, 41437, and 41439. Wind River Basin, *Plesiadapis cookei* zone: AMNH 56122, 56125, 56152, 56158, 56272, 56274, 56387, 57202, 57208, 57210, 57214, 57218, 57223, 57233, 57237–57240, 57243, 57244, 57246, 57247, 57254, 57255, 57270, 57271, 57274–57276, 57280. Laramie Basin, Wasatchian: UW 20225 and 20229. Piceance Basin, Clarkforkian: FMNH.PM 227, P 14938, 14942, 15528, 15572, 26116, 26134, and 27036.

Ectocion major (Patterson and West, 1973)
Fig. 23

Prosthecion major Patterson and West, 1973, p. 2, fig. 1–4; West, 1976, p. 44, fig. 29.
Phenacodus vortmani (in part), Rose, 1981, p. 72.
Ectocion osbornianus (in part), Rose, 1981, p. 73.

Holotype.—FMNH P26131, right dentary with P_{3-4}, and isolated M_3, left dentary with fragments of P_{3-4} and two molar fragments. Left P^{3-4} and fragments of P^1 and M^{1-2}, right P^3 fragment. The specimen also includes an isolated lower incisor, and fragments of scapula, distal humerus, proximal radius, os coxae, distal femur, and proximal tibia.

The holotype of *E. major* was found at locality Hell's Half Acre in the Piceance Basin according to the type description. The locality is Clarkforkian in age, and possibly *Plesiadapis gingerichi* zone (Archibald et al., 1987).

Age and distribution.—All three biochrones of the Clarkforkian from the Bighorn and Piceance Basin.

Diagnosis.—Large lophodont *Ectocion*, similar in size to *E. superstes* and *P. vortmani*, and larger than all other *Ectocion*. P_3 with high metaconid and weak hypoconid, unlike *E. superstes*.

Description.—Material referred to *Ectocion major* and not represented in the holotype includes complete M_{1-2} and M^{1-3}. Newly referred material from the Bighorn and Piceance Basin includes two partial upper dentitions (UM 69322 and 71357) and a P_3 (FMNH P15568). This new material increases understanding about the dental variation of the taxon. The metaconid of P_3 is larger and its hypoconid smaller than *Ectocion osbornianus* and *Ectocion superstes*. The parastyle of P^3 is larger in *Ectocion osbornianus* than in *Ectocion major* as noted by Patterson and West (1973). The paraconule of P^4 is present in some *Ectocion major* (UM 69322).

Ectocion major is larger than contemporaneous *Ectocion osbornianus* and overlaps in size with *Phenacodus vortmani* (Fig. 24). It is larger than Bridgerian *E. superstes* (Fig. 25). Morphological differences between *E. major* and *E. superstes* include the larger metaconid and weaker hypoconid of P_3. In addition, the entoconid of P_4 is absent in three of four *E. superstes* but present in all three known *E. major*. The paracristid of the lower molars is stronger in *E. major*, and the lower molars are longer. The ratio (width of trigonid)/(length) for pooled M_1 and M_2 is 0.81 in *E. major* (N = 13, SD = 0.06) and 0.84 in *E. superstes* (N = 5, SD = 0.03).

Phenacodus vortmani and *E. major* are not easily differentiated in worn specimens, but differences between the genera *Ectocion* and *Phenacodus* hold also for *E. major* and *P. vortmani*. The most obvious characters, judging from the present sample, are the lophodont dentition of *E. major*. In *E. major*, the paracristid of the lower molars extends to the base of the metaconid, and the paraconid, if present at all, is low and well separated from the metaconid. The trigonid of P_4 is wider in *E. major* than in *P. vortmani*. Parastyle and mesostyle of the upper molars are large and M^3 lacks a hypocone in *E. major* in the one available specimen (UM 71357).

Discussion.—My description of the holotype differs from that in the type description (Patterson and West, 1973). One obvious mistake in the type description is failure to mention the right M_3, while this tooth is figured and identified as part of the holotype in figures 2B and 4B of the type description. The specimen number mentioned in the caption of figure 2B in the type description also contains a typographical error, listing P26121 instead of P26131.

Referred specimens.—Bighorn Basin, *Plesiadapis gingerichi* zone: UM 71357; *Plesiadapis cookei* zone: UM 65661 and 69322; *Phenacodus-Ectocion* zone: UM 91420. Piceance Basin, Clarkforkian: FMNH.PM 225, P 14940, 14947, 15568, 15570, 15581, 15586, 26066, 26128, 26129, UCM 41235, and 41293.
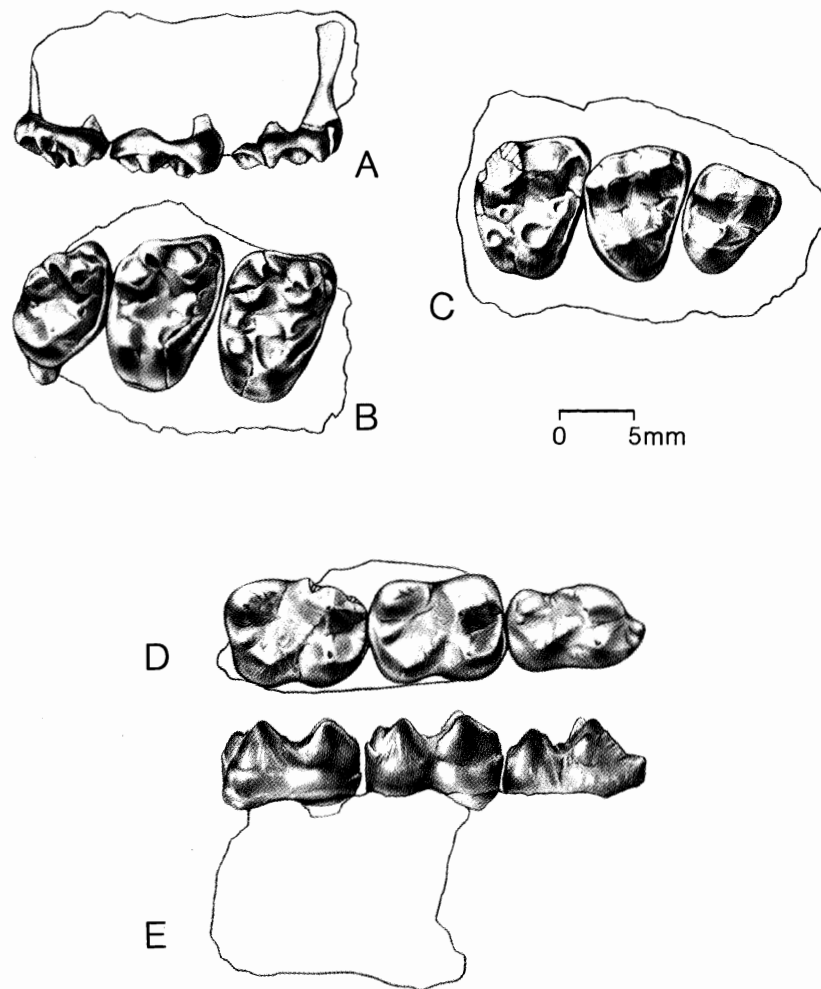
Figure 23. Dentition of *E. major* from Clarks Fork Basin. A and B, M$^{1-3}$ (UM 69322) in labial and occlusal view. C, P^3-M^1 (UM 71357) in occlusal view. D-E, P$_4$-M$_2$ (UM 65661) in occlusal and labial view.

Ectocion parvus Granger, 1915
Fig. 26

Ectocion parvus Granger, 1915, p. 353, fig. 12–13; West, 1976, p. 53, figs. 37 and 39; Rose, 1981, p. 75, fig. 34A; Gingerich, 1989, p. 49, fig. 31.

Holotype.—AMNH 16080, left dentary with M$_{1-3}$, from "Clark Fork beds, Head of Big Sand Coulee" (Granger, 1915:353). Gingerich (1982a and 1989) determined that the holotype of *E. parvus* is probably from the *Cantius torresi* zone at the end of Polecat Bench in the Bighorn Basin (UM locality SC-67).

Age and distribution.—*Phenacodus-Ectocion* zone of the late Clarkforkian through Lower *Haplomylus-Ectocion* zone of the early Wasatchian, possibly also early Clarkforkian (see below). Bighorn and Piceance Basins.

McKenna (1980) reported *E. parvus* from the Togwotee Pass Area of the Wind River Basin, but I have not seen these specimens.

Diagnosis.—Smaller than all other *Ectocion*, except *E. cedrus*. P$_3$ large, compared to lower molars, with strong hypoconid, metaconid absent unlike *E. cedrus*. P$_4$ paraconid absent and entoconid usually absent unlike *E. cedrus*.

Description.—Gingerich (1989) described what is known of the dentition of *E. parvus:* C^1 through M^3, and P$_1$ through M$_3$. *E. parvus* resembles *E. osbornianus* in shape, but is smaller (Figs. 12–17).

E. parvus and Tiffanian *E. cedrus* are similar in size. Shape differences between these two were mentioned previously. *E. parvus* is mainly known from the *Cantius torresi* zone where it occurs with *Copecion davisi*. These two
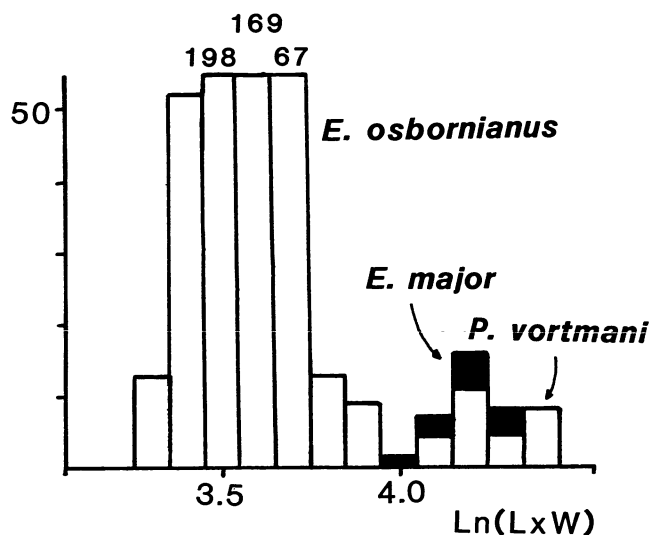
Figure 24. Histogram of natural logarithm of product of length and width (in mm) of M_1 and M_2 for Clarkforkian *Ectocion major* (black), *Ectocion osbornianus* and *Phenacodus vortmani*. Numbers over three cohorts of *E. osbornianus* represent actual number of specimens in these cohorts.
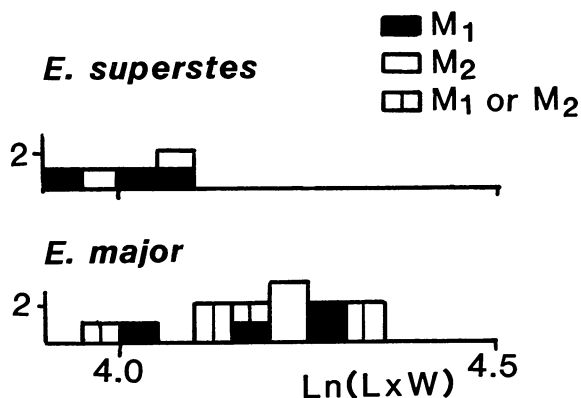
Figure 25. Histogram of natural logarithm of product of length and width (in mm) of M_1 and M_2 for Clarkforkian *E. major* and Bridgerian *E. superstes*.

phenacodontids are similar in size, and are sometimes difficult to distinguish, as pointed out by Gingerich (1989). The most diagnostic teeth are the lower premolars. P_3 of *E. parvus* is short and has a strong hypoconid, unlike that of *C. davisi*. The trigonid basin of P_4 in *Copecion* is long and narrow, unlike that of *Ectocion*. The mean of the ratio (distance between protoconid and metaconid)/(length anterior to protoconid) of P_4 is 1.00 in *E. parvus* (N=3, SD=0.16) and 0.34 in *C. davisi* (N=2, SD=0.01).

Principal component analysis was used to further explore differences between P_4s of *Ectocion parvus* and *Copecion*

davisi. Five measures of P_4 were analyzed (length, width, length anterior to protoconid, length anterior to metaconid, and distance between protoconid and metaconid). The three measures involving shape of the trigonid basin load on PC-1. PC-1 scores of three specimens of *E. parvus* range from 3.3 and 4.0, and in two specimens of *C. davisi* the scores are 5.5. The entoconid of P_4 is usually strong in *E. parvus* (although absent in UM 82386), but is usually absent in *Copecion*.

Ectocion parvus and *Copecion davisi* are easily distinguished on the basis of premolars. Differences between the lower molars of the taxa are more subtle, and identification of incomplete or worn dentitions is not always possible. Teeth of *Ectocion* are less bunodont than those of *Copecion*. This is most apparent in the trigonid basin: the furrow between protoconid and metaconid is typically U-shaped in *Ectocion*, whereas in *Copecion* it is V-shaped. The protoconid and metaconid may be farther apart in *Ectocion*: (distance between metaconid and protoconid)/(width of trigonid) of M_2 is 0.41 in *E. parvus* (N = 1) and 0.46 in *C. davisi* (N = 2). Gingerich (1989) pointed out that the paracristid usually descends to the base of the metaconid in *Ectocion parvus* but ascends that cusp in *Copecion*. In some *Ectocion* the paracristid does ascend the metaconid (UM 83474, 83626, and 83657).

E. parvus has a shorter M^2 with a larger mesostyle and a larger M^3 than *Copecion* (Table 4). Gingerich (1989) noted that the furrow in the lingual outline of the upper molars between the protocone and hypocone is usually present in *Copecion* but not in *Ectocion*. Although this character usually corroborates the cited characters, it is at odds with these in some cases.

Discussion.—Van Valen (1978) synonymized *Meniscotherium priscum* Granger, 1915 with *Ectocion parvus*. Only molars are known for *Meniscotherium priscum* but they display the characters that differentiate *Meniscotherium* from *Ectocion* as described above. Rose (1981) described differences between the holotypes of *E. parvus* and *M. priscum* in detail.

Ectocion parvus in the Bighorn Basin is abundant only in a short interval: the *Cantius torresi* zone of the early Wasatchian. One specimen occurs in the late Clarkforkian (UM 65519, the small outlier of scatter diagrams of M^1 and M^2 of Figs. 16 and 17) and one in the Lower *Haplomylus-Ectocion* zone. *E. osbornianus* has the reverse distribution: it is common in the *Phenacodus-Ectocion* and Lower *Haplomylus-Ectocion* zone, but rare in the *Cantius torresi* zone.

West (1976) and Kihm (unpubl., 1984) reported *Ectocion parvus* from the Piceance Basin. These specimens are from localities that were considered early Clarkforkian by Archibald et al. (1987). Piceance Basin *E. parvus* predates Bighorn Basin *E. parvus* if the age assessment is correct.

Referred specimens.—Bighorn Basin, *Phenacodus-Ectocion* zone: UM 65519; *Cantius torresi* zone: UM 66138, 66140 (in part), 66617 (in part),
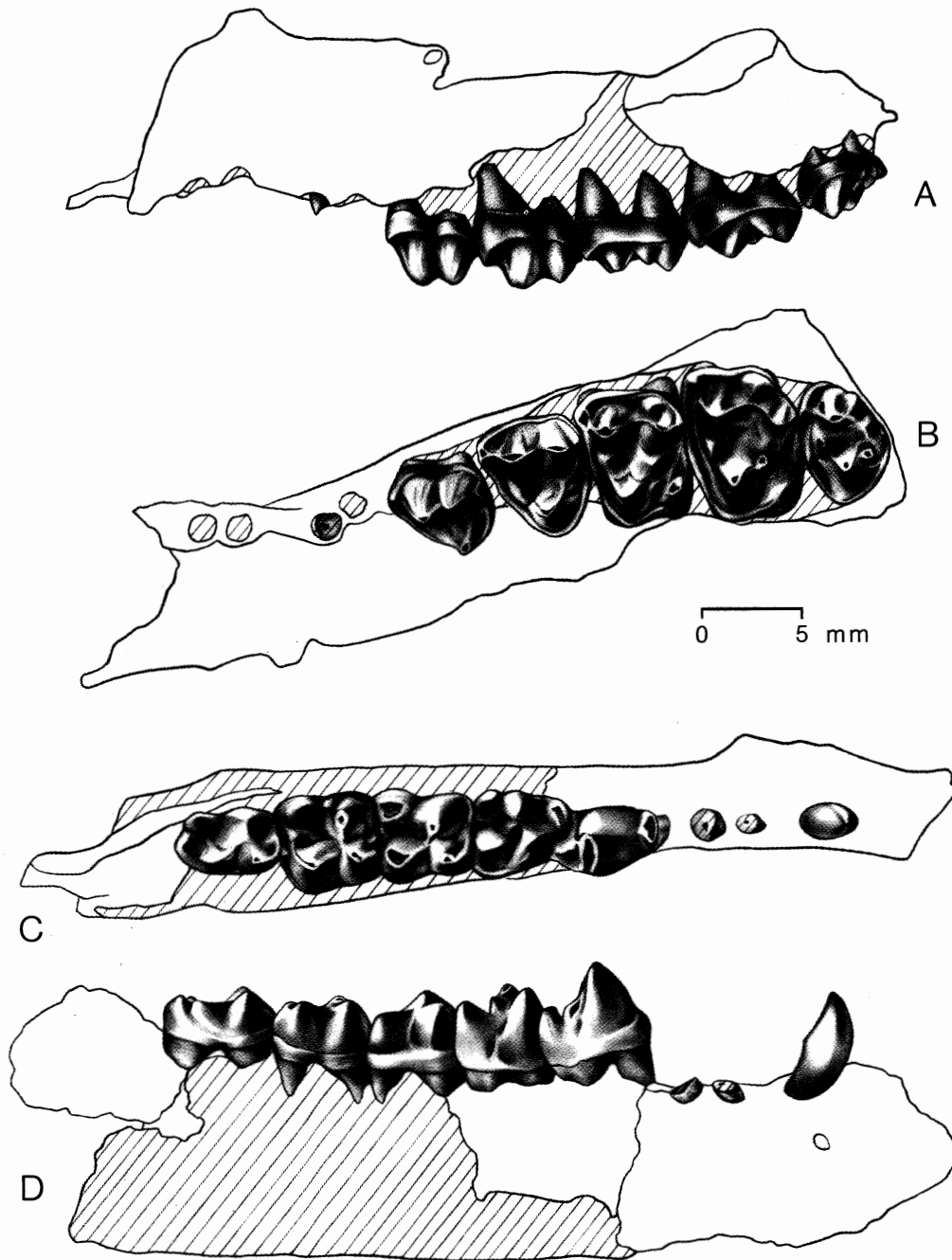
Figure 26. Dentition *Ectocion parvus* from Clarks Fork Basin (UM 77202). A and B, P^3-M^3 in labial and occlusal view. C and D, P_1, P_3-M_3 in occlusal and labial view. Reprinted from Gingerich (1989).

71768 (in part), 74076, 76235, 77202, 79884, 82380, 82381, 82384, 82386, 83474, 83476, 83618 (in part), 83623 (in part), 83626, 83636 (in part), 83660, 83824, 83871, 85594, 85595 (in part), 85668, 86000, 86570, 86572 (in part), 87338, 87342, 87354, 87859 (in part), 92423, and YPM-PU 18153; Lower *Haplomylus-Ectocion* zone: UM 80761. Piceance Basin, Clarkforkian: FMNH PM209, P15536.

Ectocion superstes Granger, 1915
Fig. 27

Ectocion superstes (in part), Granger, 1915, p. 352, fig. 12–13.
Ectocion superstes, West, 1976, p. 58, fig. 37a.
Phenacodus vortmani (in part), Guthrie, 1971, p. 81.

Table 4. Comparison of *Ectocion parvus* and *Copecion davisi*. Characters are: Length/width ratio of M^2; height of mesostyle of M^2; presence or absence of lingual furrow on M^2; length and width product of M^3.

Specimen	M^2 L/W	M^2 mesostyle	M^2 furrow	M^3 L × W
Ectocion parvus				
UM 66140				31.9
UM 77202L	0.68	1.7	A	24.8
UM 77202R	0.71	1.2	A	
UM 83824	0.71	1.3	P	
UM 85594	0.69	Large	P	
Copecion davisi				
UM 66611	0.72	1.0	P	
UM 71769	0.79	Small	P	23.4
UM 83634	0.76	1.1	P	
UM 83663		Small		21.1
UM 83781				18.4
UM 83823	0.75	0.9	P	21.8
UM 92348	0.75	0.9	A	20.5

Holotype.—AMNH 233A, dentary with C_1, P_3-M_3, from "Lost Cabin Beds, Wind River Basin, Wyo. J. L. Wortman, 1891" (Granger, 1915:352). All specimens of *E. superstes* for which adequate locality data is available are associated with a fauna from the *Palaeosyops* zone (Stucky, pers. comm., 1988). It is therefore likely that the holotype is also from this zone.

Age and distribution.—*Palaeosyops* zone of the Bridgerian (Krishtalka et al., 1987) of the Wind River Basin.

Diagnosis.—Similar in size to *E. major*, larger than other *Ectocion*. P_3 large with strong hypoconid and no metaconid, unlike *E. major*. P_4 metaconid and protoconid well separated. Lower molars with weak paracristid. P^4 paracone and metacone well separated.

Description.—P_1 to M_3 and P^4 to M^3 are known for *E. superstes*. The mandibular symphysis is fused in the only specimen in which it is preserved. The alveoli of the lower canines of this specimen are larger than in other *Ectocion* (CM 43393).

E. superstes is larger than early Wasatchian *E. osbornia- nus*. Granger (1915) described morphological differences based on the holotype only, but noted that P_3 was longer than P_4, and that the paracristid of P_4 was weak and the entoconid high. The ratio (length of P_3)/(length of P_4) is 1.09 in the holotype of *E. superstes*, but only 0.89 in a referred specimen (CM 43184). The mean of this ratio is 0.99 in Wasatchian *E. osbornianus* (N = 126; SD = 0.06; range: 0.80–1.21). This ratio does not distinguish between the two taxa. The entoconid of P_4 is present in 33% of Wasatchian *E. osbornianus* (N = 180), but present in all *E. superstes* (N = 3). The characters of the paracristid of P_4 can only be evaluated when more material becomes available. Differences between *E. superstes* and *E. major* were described before.

Discussion.—Granger (1915) tentatively referred two specimens from early Wasatchian strata of the Bighorn Basin to *Ectocion superstes*. Simpson (1943) included only one of these in *E. superstes*, and West (1976) pointed out that this specimen is probably *E. osbornianus* as well. I share West's opinion. McKenna (1960) and Guthrie (1971) suggested that the holotype was probably an aberrant specimen of *P. vortmani*, but the sample of *Ectocion superstes* recently obtained in the Wind River Basin establishes the distinctiveness of the taxon beyond doubt.

Referred specimens.—Wind River Basin, *Palaeosyops* zone: CM 22351, 22354, 22356, 31015, 43184, 43393, 43665, 44817, and UCM 43184.

Phenacodus Cope, 1873

Phenacodus Cope, 1873a, p. 3; Cope, 1885, p. 428; Granger, 1915, p. 332; West, 1973, p. 135; West, 1976, p. 19; Rose, 1981, p. 70.
Opisthotomus Cope, 1875, p. 15.
Eohyus (in part) Marsh, 1894, p. 259.
Almogaver Crusafont and Villalta, 1955, p. 9.

Type of genus.—*Phenacodus primaevus* Cope, 1873a.

Referred taxa.—*P. vortmani* (Cope, 1880); *P. trilobatus* Cope, 1882f; *P. intermedius* Granger, 1915; *P. teilhardi* Simpson, 1929b; *P. grangeri* Simpson, 1935c; *P. matthewi* Simpson, 1935c; *P. condali* (Crusafont and Villalta, 1955); *P. bisonensis* Gazin, 1956a; *P. magnus* new; *P. lemoinei* new. Taxa restricted to the holotype only, and those considered *incertae sedis* are listed below.

Age and distribution.—Tiffanian through Bridgerian land-mammal ages of Western North America. Dormaalian (Sparnacian) through Robiacian (Lutetian) of Western Europe.

Diagnosis.—Differs from *Ectocion* in having P_3 with large metaconid, hypoconid weak or absent. P_4 short unlike *Copecion*. Differs from *Ectocion* by bunodont molars, and paracristid ending usually high on the lingual side of the molars. P^1 single rooted, unlike *Ectocion* and molar mesostyle smaller. Differs from *Tetraclaenodon* in large metacone of P^4. Parastyle and mesostyle of upper molars usually weaker than *Ectocion*, but stronger than *Tetraclaenodon*. Hypocone strong in M^{1-2} and usually present in M^3 unlike *Ectocion*.

Description.—*Phenacodus* is the only phenacodontid for which cranial and postcranial osteology are adequately known. *Phenacodus* is bunodont, its paracristid ascends the metaconid, and the mesostyle is large but smaller than that of *Ectocion*. The mandibular symphysis is unfused in most referred taxa. Size is the character that best distinguishes between different *Phenacodus*. *Phenacodus* is less curso- rial than *Ectocion* and *Copecion*. It has a wide rostrum and inflated frontal sinuses, possibly in males only, and may have had a short trunk (see Chapter VII).

Discussion.—I follow Granger (1915) who restricted *Phenacodus astutus* to the holotype of *Opisthotomus astu- tus* Cope, 1875. The holotype and only specimen of *P.*
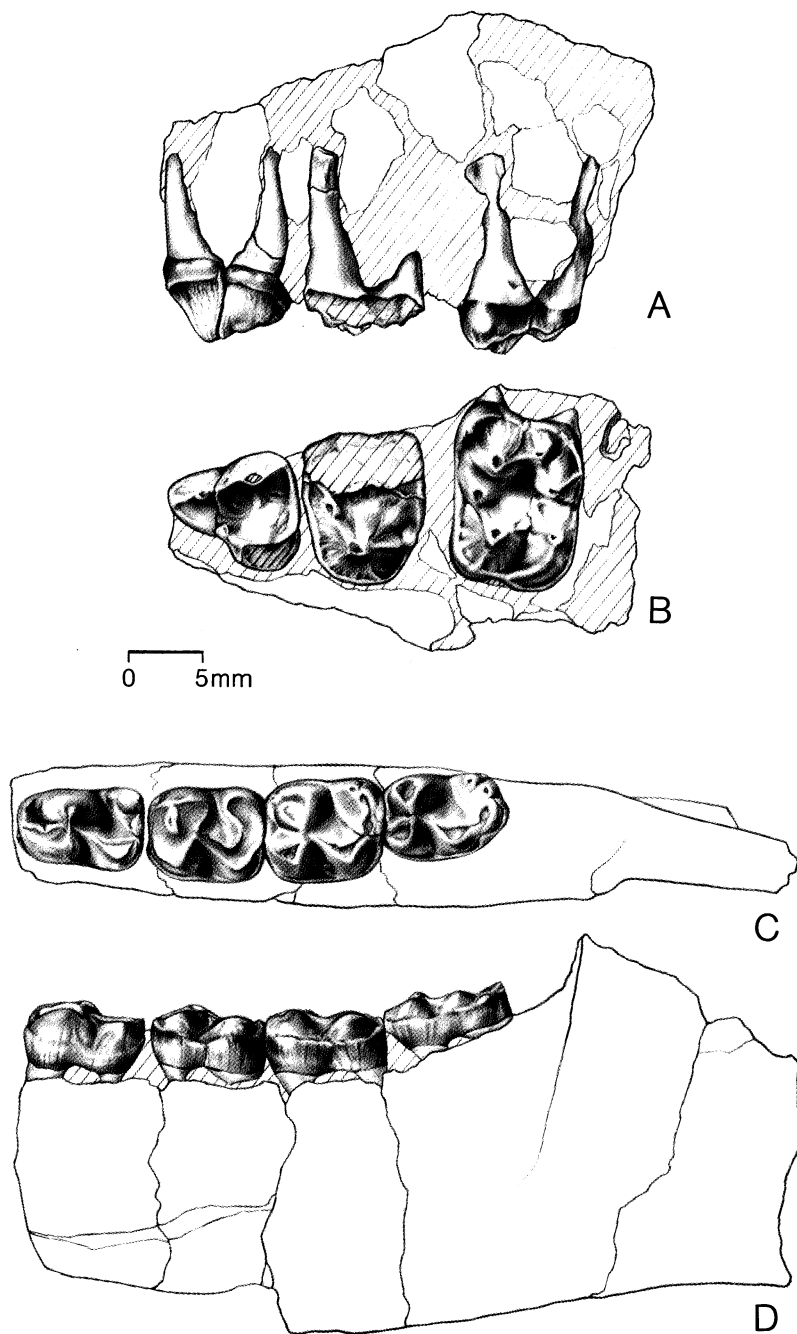
Figure 27. Dentition of *Ectocion superstes* from the Wind River Basin. A and B, P³-M¹ (CM 37326) in labial and occlusal view. C and D, P$_4$-M$_2$ (CM 43393) in occlusal and labial view.

astutus consists of two teeth that are questionably associated according to Granger (1915), and both are lost. Granger (1915) suggested synonymy of the genotype of *Eohyus*, *Eohyus distans* Marsh, 1894, with *Phenacodus primaevus*. Lucas (1980) supported this claim and also fig-

ured and discussed the holotype and only specimen of *Eohyus distans*. The specimen is an M³ (YPM 11889) from the Wasatchian of the San Juan Basin that is too fragmentary for identification beyond *Phenacodus*. *Almogaver* Crusafont and Villalta, 1954, was considered a primate in the

type description. The type and only specimen differs from other European *Phenacodus* only in characters that are well within the range of better known *Phenacodus*. At present I consider *Almogaver* and *Phenacodus* synonymous.
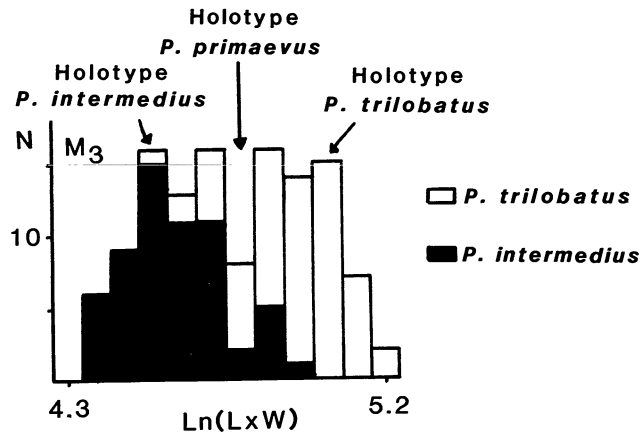
Figure 28. Histogram of natural logarithm of product of length and width of M_3 of Wasatchian *P. intermedius, P. trilobatus,* and holotype of *P. primaevus.* Note the broad area of overlap in size between *P. intermedius* and *P. trilobatus;* M_3 is usually insufficient as a basis for identification. Also notice the intermediate position of the holotype of *P. primaevus.*

The holotype of *Phenacodus primaevus* Cope, 1873 is a poorly preserved M_3 (AMNH 4408) from late Wasatchian rocks near Evanston, Wyoming. The specimen was mistaken for an M^3 in Cope's (1873a) original description. The type description also spelled the name as *Phenacodus primaeous,* although Cope used *P. primaevus* in all later publications. In spite of renewed collecting effort at the presumed type locality by M. C. McKenna (pers. comm., 1988), no additional specimens of *Phenacodus* have been collected. The holotype is intermediate in size between *P. intermedius* and *P. trilobatus* (Fig. 28). Because of the overlap in M_3 size between these two taxa, the holotype of *P. primaevus* cannot be positively identified as either, and I therefore restrict the name to the holotype only. Because the name *P. primaevus* has been used for both taxa identified here as *P. trilobatus* and *P. intermedius* (e. g., by Guthrie, 1971, and Schankler, 1981), this has the additional benefit of limiting the use of an ambiguous name to a single specimen.

The holotype and only specimen of *Phenacodus omnivorus* Cope, 1874, is a non-diagnostic M^3. I restrict *Phenacodus omnivorus* to the holotype only. The specimen described as holotype of *Phenacodus nuniensis* Cope, 1885, includes postcranial material of several individuals of *Phenacodus* as well as mesonychids (Granger, 1915). *Phenacodus nuniensis* should be abandoned. I follow Granger (1915), who cited *Phenacodus sulcatus* Cope, 1874, as *incertae sedis. Phenacodus laticuneus* Cope,

1882a, was transferred to *Diacodexis* by Cope (1882i), and *Phenacodus macropternus,* Cope (1882a) is now considered an artiodactyl, *Bunophorus macropternus.* The holotype of *Phenacodus hemiconus* Cope, 1882a is a M^{2-3} of a large phenacodontid. The specimen is not diagnostic. Savage and Russell (1983:45) cited *Phenacodus praecox,* which is a misprint of *Phenacolemur praecox.*

A dentary fragment with P_{3-4} and a fragment of M_1, and an isolated P_4 were described as the holotype of *Phenacodus villaltae* and *Phenacodus* cf. *teilhardi* respectively (Crusafont Pairo, 1956a, b). Both specimens are of similar size, were found in the same area of the Tremp Basin, and are apparently also similar in morphology. I have not seen either of these specimens, but the figure of the jaw (Crusafont Pairo, 1956b, fig. 1) leaves some doubt as to the generic identification. The shape of P_3 and the paracristid of M_1 are more reminiscent of *Ectocion,* if a phenacodontid at all.
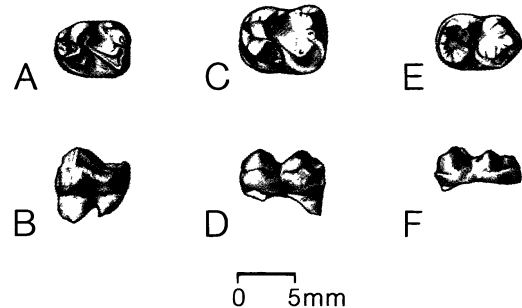
Figure 29. Dentition of *Phenacodus matthewi* from Keefer Hill. A and B, P_4 (CM 34292) in occlusal and labial view. C and D, M_1 or M_2 (CM 34289) in occlusal and labial view. E and F, M_3 (CM 34287) in occlusal and labial view.

Phenacodus matthewi Simpson, 1935
Fig. 29

Phenacodus matthewi Simpson, 1935c, p. 24, fig. 12; West, 1976, p. 20, fig. 7.
Phenacodus gidleyi Simpson, 1935c, p. 25, fig. 13.
Ectocion cf. *E. montanensis,* Schiebout, 1974, p. 30, fig. 22f-h, 23d-e.

Holotype.—AMNH 17191, right dentary with M_{2-3}. The holotype is from the late Tiffanian of the San Juan Basin.

Age and distribution.—*Plesiadapis praecursor* through *P. churchilli* or *P. simonsi* zones of the Tiffanian from the Wind River and San Juan Basins, and Big Bend National Park.

Diagnosis.—Smaller than any other *Phenacodus.* Parastyle and mesostyle larger than other *Phenacodus.*

Description.—Two P_4s, several lower molars, and one upper molar are known for *P. matthewi.* The taxon is best differentiated from contemporary *Phenacodus* by its small size (Fig. 30). The single upper molar known for *P. mat-*
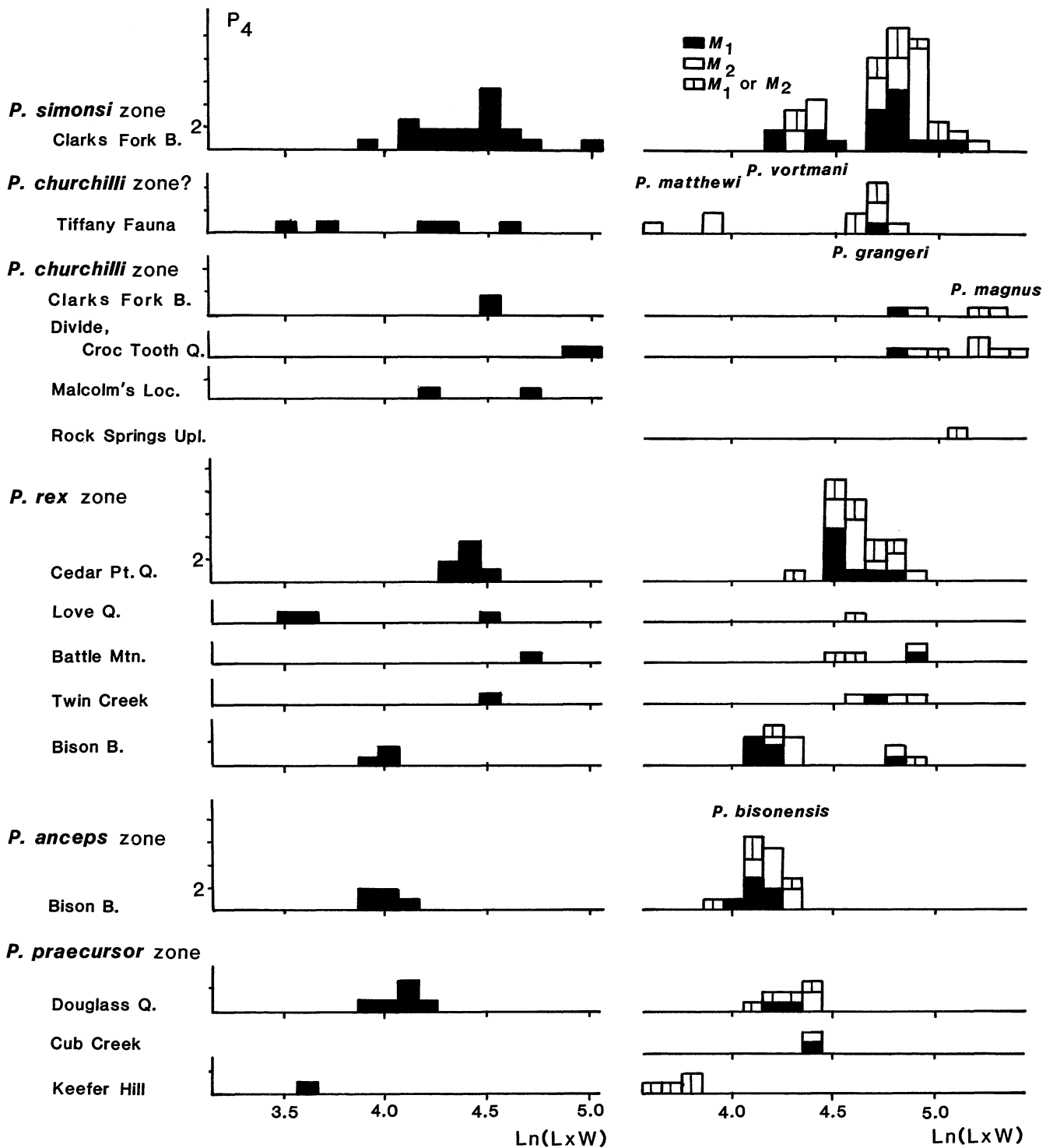
Figure 30. Histograms of natural logarithm of product of length and width (in mm) of P_4, M_1, and M_2 for some Tiffanian *Phenacodus matthewi*, *P. bisonensis*, *P. vortmani*, *P. grangeri*, and *P. magnus*. *Plesiadapis praecursor* zone: Keefer Hill (Wind River Basin), Cub Creek (Clarks Fork Basin), and Douglass Quarry (Crazy Mountains Basin). *P. anceps* zone: Saddle locality and others (Bison Basin). *P. rex* zone: Ledge locality and others (Bison Basin), Twin Creek (Fossil Basin), Battle Mountain Local Fauna (Hoback Basin), Love Quarry (Wind River Basin), and Cedar Point Quarry (Bighorn Basin). *P. churchilli* zone: locality east of Rock Springs Uplift (Washakie Basin), Malcolm's locality (Wind River Basin), Divide and Croc Tooth Quarries (Bighorn Basin), and many localities in the Clarks Fork Basin. Possibly *P. churchilli* zone: Tiffany Fauna (San Juan Basin). *P. simonsi* zone: Clarks Fork Basin.

thewi (TMM-TAMU 40536–167) has a larger parastyle and mesostyle than is typical in other *Phenacodus*, but within the total range of variation. The importance of this difference can only be evaluated after more material is recovered.

Discussion.—The type description gives unsatisfactory locality information for the holotype of *P. matthewi:* "Tiffany Beds, Colorado" (Simpson, 1935c:24). The label of the specimen bears partially conflicting data in three different handwritings. According to Granger's 1916 fieldbook the locality is: "2 mi. N. of Arboles—E. side of Piedra R." This information was copied to the specimen label, but later: "Mason Pocket?" was added. West (1976:20) cited "Mason Pocket" as the type locality for *Phenacodus matthewi*, probably on the basis of the added information on the label. According to Granger (1917), the Mason Pocket locality is in Sec. 20, T33N, R6W; it is therefore not two miles north of Arboles. Granger's (1917) faunal description lists that "Phenacodonts, 3 species" (p. 828) were surface finds, distinct from the "mass of soft uniform clay" (p. 827) which was called Mason Pocket later. These phenacodontids are probably the ones described as *Phenacodus grangeri*, *P. matthewi*, and *P. gidleyi* by Simpson (1935c). I conclude that the type specimen of *P. matthewi* was found north of Arboles on the east bank of the Piedra River, and is not from Mason Pocket.

The holotype of *P. gidleyi* includes worn P_4, M_2, and M_3. The molars are slightly smaller than the holotype of *P. matthewi*, but they are morphologically similar. The paraconid of P_4 is worn, but apparently larger than in a P_4 from Keefer Hill here referred to *P. matthewi* (CM 34292). The size of the paraconid of P_4 is variable in *Phenacodus*, and no other morphological differences are obvious. I consider *P. gidleyi* synonymous with *P. matthewi*.

P. matthewi is contemporaneous with and slightly larger than *Ectocion collinus*, but the morphological differences between the genera serve to distinguish the taxa: teeth of *Phenacodus matthewi* are more bunodont and the molar paracristid ascends the metaconid. The morphology of P_4 is the best character to distinguish between similar sized *Copecion brachypternus* and *P. matthewi*. Morphological differences between *P. matthewi* and other *Phenacodus* cited by Simpson (1935c) and West (1976) are not apparent on the basis of the larger sample available now.

Phenacodus matthewi is known from the localities Keefer Hill and Love Quarry in the Wind River Basin, from several localities in the Big Bend National Park and from the type sample.

Referred specimens.—Wind River Basin, *Plesiadapis praecursor* zone: CM 34287–34292; *Plesiadapis rex* zone: AMNH 57333, 89689, and 89690. San Juan Basin, late Tiffanian: AMNH 17193 (holotype *P. gidleyi*) and 56284. Big Bend National Park, *Plesiadapis rex* zone: TMM-TAMU 40536–167, 41365–16, 41365–307, 41365–784, and 41365–825.

Phenacodus bisonensis Gazin, 1956
Fig. 31

Phenacodus? *bisonensis* Gazin, 1956a, p. 44, pl. 10:1–3.
Phenacodus or *Gidleyina*, J. A. Wilson, 1967, p. 162, fig. 113 (figure printed with caption of fig. 114).
Phenacodus bisonensis, West, 1971, p. 14, fig. 8c; West, 1976, p. 21, fig. 8; Krause and Gingerich, 1983, p. 179, fig. 18.
Phenacodus cf. *P. matthewi*, Schiebout, 1974, p. 29, fig. 22d-e, 23c.

Holotype.—USNM 20564, right maxilla with P^4-M^2, and probably associated left maxilla with M^{1-2}, from the "vicinity of Saddle locality" (Gazin, 1956a:44), Bison Basin. This locality yields fossils from the *Plesiadapis anceps* zone (Gingerich, 1976a).

Age and distribution.—*Plesiadapis praecursor* through *Plesiadapis rex* zones of the Tiffanian from the Crazy Mountains, Bighorn, Bison, and Washakie Basins, and Big Bend National Park.

Diagnosis.—Intermediate in size between *P. matthewi* and *P. grangeri*, similar in size to *P. vortmani*. Differs from *P. vortmani* by the narrow talonid basin of P_4, and the common presence of an entoconid. P^4 metaconule often present, unlike *P. vortmani*.

Description.—Only dental material is known for *Phenacodus bisonensis*, it includes P_2-M_3, D_{3-4}, P^3-M^3, and D^4. *P. bisonensis* is smaller than contemporaneous *P. grangeri* and late Tiffanian and Clarkforkian *P. vortmani*. The size ranges of *P. bisonensis* and *P. vortmani* overlap (Figs. 32–35). On the basis of the present sample, *P. bisonensis* differs from *P. vortmani* in the narrow talonid basin of P_4 ("P_4 weakly basined" of Gazin, 1956a:45). *P. bisonensis* differs from *P. grangeri* and *P. vortmani* in the percentages of incidence of certain cusps. The entoconid of P_4 is present in 59% of the specimens (N = 17), in 43% of *P. grangeri* (N = 28), but is absent in all Tiffanian and early Clarkforkian *P. vortmani* (N = 6). The metaconule of P^4 is present in 32% of *P. bisonensis* (N = 12), in 36% of *P. grangeri* (N = 22), and in only 3% of *P. vortmani* (N = 33).

Discussion.—The morphological similarity between *P. bisonensis* and *P. vortmani* is considerable, and positive separation of these two taxa is often impossible. The diagnosis of *P. bisonensis* given by West (1976) follows Gazin's (1956a) original diagnosis closely, and does not compare *Phenacodus bisonensis* with *P. vortmani*. The sample of *P. bisonensis* studied by these authors was small, and some of the described differences, such as the incidence of the paraconid on lower molars and position of this cusp on P_4, do not hold for the larger sample that is now available. Both Gazin (1956a) and West (1976) claimed that the lower premolars of *P. bisonensis* are less "progressive" than those of other *Phenacodus*. This may be based on the absence of a metaconid on P_3 in one of the few specimens available at the time of their work (USNM 20567). The metaconid is present on P_3 of most other specimens (e. g., AMNH 92096). The height of the mesostyle of the upper molars is similar in *P. bisonensis* and *P. vortmani*. Differentiating between *P. vortmani* and *P. bisonen-*
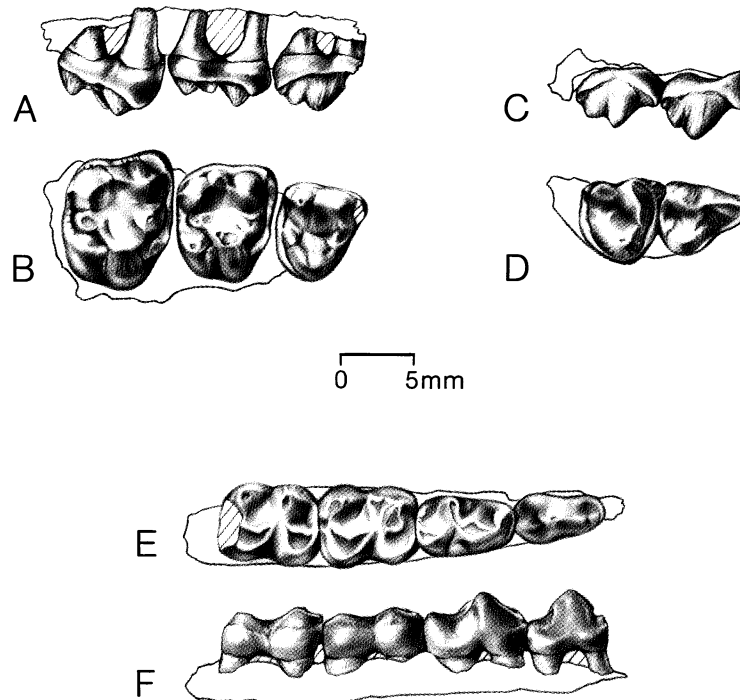
Figure 31. Dentition of *Phenacodus bisonensis* from Bison Basin Ledge locality. A and B, P⁴-M² (USNM 20564), holotype in labial and occlusal view. C and D, P³⁻⁴ (USNM 20566) in labial and occlusal view. E and F, P_3-M_2 (USNM 20567) in occlusal and labial view.

sis remains problematic until late Tiffanian and early Clarkforkian phenacodontid samples are enlarged.

Referred specimens.—Crazy Mountains Basin, *Plesiadapis praecursor* zone: YPM-PU 14633, 14634, 23694, UM 89068–89102, UM field number 83–64, 83–170, 83–217, 83–491, 83–605, 84–609, and 85–746; *Plesiadapis rex* zone: UM field number 85–310, 85–311, 85–312, 85–322, 85–330, 85–333, 85–334, 85–339, 86–591, 86–596, and 86–598. Bighorn Basin, *Plesiadapis praecursor* zone: UM 80167. Bison Basin, *Plesiadapis anceps* zone: AMNH 86706, 92096, 92109, 92140, 92156, 92158, CM 18432, 18730, 18733, 18775, 29243, 40557, 40558, 40592–40594, MCZ 18735, 18738, UCM 40425, 40428, 48001, UCMP 111945–111947, 111964, 114309, 114131, 133946, UW 1094, 1095, 1097, 1098, 1101, 2268, 12985, and 12987; *Plesiadapis rex* zone: UCM 40432, 49370, AMNH 86650, 86656, USNM 20564–20569, 26325, 40675, 406069–405074, 405076; Tiffanian: CM 29432, MCZ 7384, 18731, 18737, USNM 20625–20627, 406069, 406070, 406072–406074. Big Bend National Park, *Plesiadapis rex* zone: TMM-TAMU 41048–4, 40148–6, 41365–569, 41366–27; Tiffanian: TMM-TAMU 40147–19 (in part).

Phenacodus grangeri Simpson, 1935
Figure 36

Phenacodus grangeri Simpson, 1935c, p. 23, fig. 10–11; West, 1971, p. 12, fig. 9; Schiebout, 1974, p. 28, fig. 22a-c, 23a-b.
Phenacodus primaevus (in part), Gazin, 1952, p. 61; Van Valen, 1978, p. 58; West, 1976, p. 33, fig. 19c; Holtzman, 1978, p. 58, fig. 11.20; Winterfeld, 1982, p. 100.
?*Phenacodus sp.*, Gazin, 1956a, p. 46, pl. 10:4–5.

Phenacodus sp., Gazin, 1956b, p. 710.
Tetraclaenodon transitus Dorr, 1958, p. 1225, pl. 2:1–4.
Tetraclaenodon sp. indet., Dorr, 1958, p. 1225.
Phenacodus cf. *P. grangeri*, Wilson, 1967, p. 162, fig. 114 (figure printed with caption of fig. 115).
Phenacodus cf. *primaevus*, Krishtalka et al., 1975, p. 209.
Phenacodus bisonensis (in part), Winterfeld, 1982, p. 99.

Holotype.—AMNH 17185, right maxilla with M¹⁻², and labial fragment of M³, from "2 mi. N. of Arboles, Colo." of the northeastern San Juan Basin. This locality is one of the sites yielding the Tiffany Fauna and dates from the *Plesiadapis churchilli* zone (Gingerich, 1976a).

Age and distribution.—*Plesiadapis rex* through *Plesiadapis simonsi* zones of the Tiffanian, possibly also *P. praecursor* zone (see discussion) of the Williston, Bighorn, Wind River, Green River, Fossil, Bison, Washakie, and San Juan Basins, and Big Bend National Park.

Diagnosis.—Comparable in size to *Phenacodus intermedius*, smaller than *P. magnus*, larger than *P. vortmani*. P_4 trigonid basin wider than *P. magnus*. Lower molar trigonid short. P⁴ wider than long, unlike *P. intermedius*.

Description.—Among permanent teeth, C_1-M_3, C¹, P³-M³ are known for *P. grangeri*. West (1971) described the deciduous dentition. *Phenacodus grangeri* is smaller than contemporaneous *P. magnus*. This size difference is best
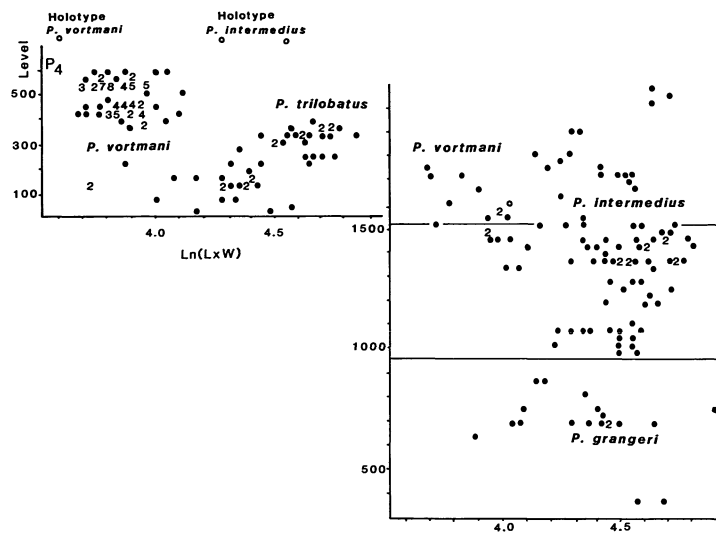
Figure 32. Scatter diagrams of natural logarithm of product of length and width (in mm) of P₄ for Bighorn Basin *Phenacodus vortmani*, *P. grangeri*, *P. intermedius*, and *P. trilobatus*. Ordinate is level (in meters) in central Bighorn Basin section (left) and Clarks Fork Basin section (right). Open circles at top of scatterplots are values for Wasatchian holotypes of *P. vortmani* from the Wind River Basin, and *P. intermedius* (left and right dentaries) from Bighorn Basin. Horizontal lines represent zonal boundaries between Tiffanian, Clarkforkian, and Wasatchian.
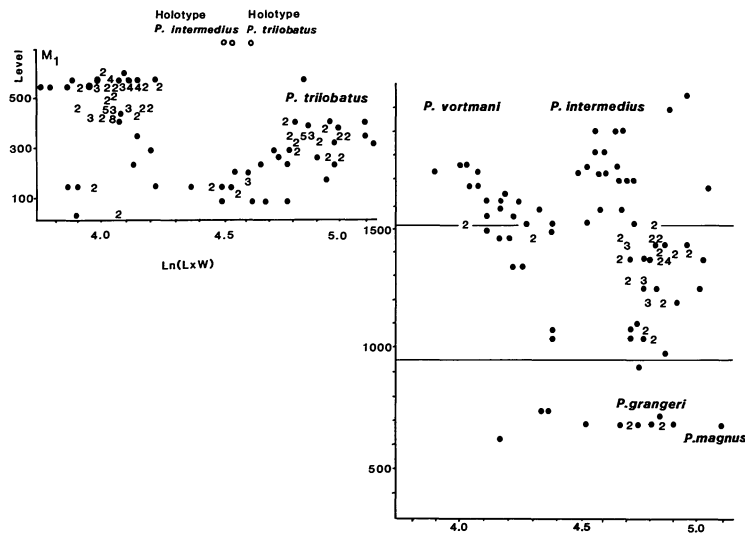
Figure 33. Scatter diagrams of natural logarithm of product of length and width (in mm) of M₁ for Bighorn Basin *Phenacodus vortmani*, *P. grangeri*, *P. magnus*, *P. intermedius*, and *P. trilobatus*. Ordinate is level (in meters) in central Bighorn Basin section (left) and Clarks Fork Basin section (right). Open circles at top of scatterplots are values for Wasatchian holotypes of *P. intermedius* (left and right dentaries) and *P. trilobatus* from Bighorn Basin. Horizontal lines represent zonal boundaries between Tiffanian, Clarkforkian, and Wasatchian.
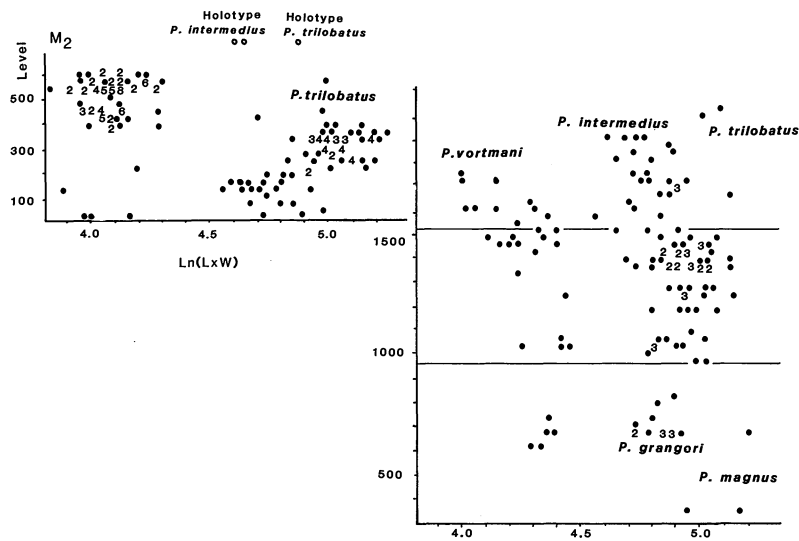
Figure 34. Scatter diagrams of natural logarithm of product of length and width (in mm) of M_2 for Bighorn Basin *Phenacodus vortmani, P. grangeri, P. magnus, P. intermedius,* and *P. trilobatus*. Ordinate is level (in meters) in central Bighorn Basin section (left) and Clarks Fork Basin section (right). Open circles at top of scatterplots are values for Wasatchian holotypes of *P. intermedius* (left and right dentaries) and *P. trilobatus* from Bighorn Basin. Horizontal lines represent zonal boundaries between Tiffanian, Clarkforkian, and Wasatchian.
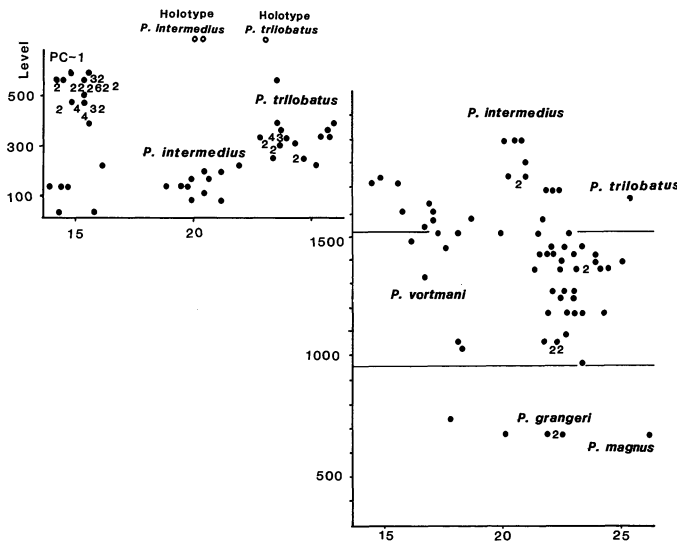
Figure 35. Scatter diagrams of principal component 1 of six lower molar measures (originally measured in mm) for Bighorn Basin *Phenacodus vortmani, P. grangeri, P. magnus, P. intermedius,* and *P. trilobatus*. Dental measures analyzed are length, trigonid width and talonid width of M_{1-2}. Ordinate is level (in meters) in central Bighorn Basin section (left) and Clarks Fork Basin section (right). Open circles at top of scatterplots are values for Wasatchian holotypes of *P. intermedius* and *P. trilobatus* from the Bighorn Basin. Horizontal lines represent zonal boundaries between Tiffanian, Clarkforkian, and Wasatchian.
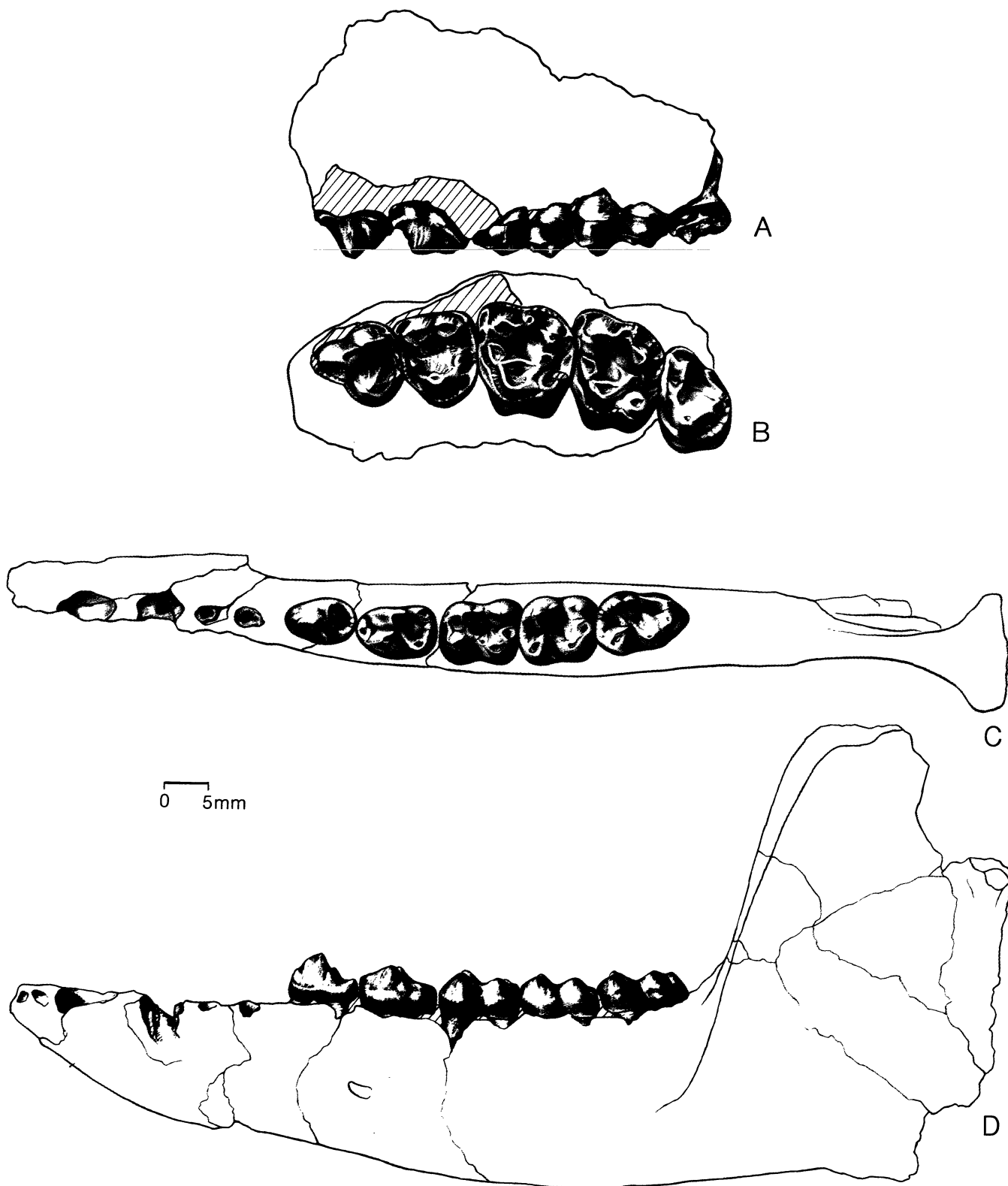
Figure 36. Dentition of *Phenacodus grangeri*. A and B, P³-M³ (YPM-PU 19924), labial and occlusal view. C and D, P₃-M₃ (YPM-PU field number 101–72), occlusal and labial view. Both specimens are from the *Plesiadapis rex* zone of Cedar Point Quarry.

demonstrated when measurements on different teeth are combined in principal component analysis, individual teeth are sometimes not identifiable (Figs. 30 and 35). A shape difference between these two taxa is the inflated appearance of the cusps of *P. magnus*. The distance between protoconid and metaconid of P_4 may be less in *P. magnus* than in *P. grangeri:* the ratio (distance protoconid-metaconid)/(length) of P_4 is 0.23 in the two specimens of *P. magnus* for which it can be calculated. The mean of this ratio is 0.27 in *P. grangeri* (N = 10; SD = 0.04). The relevance of this difference can only be evaluated when more specimens become available.

The main difference between Tiffanian *P. grangeri* and Clarkforkian and Wasatchian *P. intermedius* is the shape of P^4. This tooth is usually short and wide in *P. grangeri*, whereas it is usually approximately as long as it is wide in *P. intermedius* (Table 5).

Table 5. Ratio of width and length of P^4 in North American *Phenacodus*.

	P^4 W/L		
	N	Mean	SD
P. bisonensis	9	1.08	0.06
P. grangeri	28	1.18	0.09
P. magnus	11	1.14	0.08
P. vortmani	63	1.12	0.07
P. intermedius	58	1.07	0.07
P. trilobatus	14	1.05	0.06

Discussion.—The type sample of *P. grangeri* is from the Tiffany fauna of the northern San Juan Basin. The sample has been enlarged since Simpson's (1935c) work on this fauna (e.g., AMNH 56278, UM 71351).

Dorr (1958) described *Tetraclaenodon transitus* from the Battle Mountain Local Fauna on the basis of a poorly preserved skull and isolated P^2. Dorr (1958) noted that the taxon was morphologically intermediate between *Tetraclaenodon* and *Phenacodus,* and described differences with all taxa included in *Tetraclaenodon.* His comparisons with *Phenacodus* included mainly Clarkforkian specimens, and this is partly the reason for Dorr's assignment of the taxon to *Tetraclaenodon.* Dorr (1958) cited the broad P^4 as one of the differences between *T. transitus* and Clarkforkian *Phenacodus.* As pointed out before, Tiffanian *P. grangeri* differs from Clarkforkian *P. intermedius* in this respect. Gingerich (1976a) established that the Battle Mountain Local Fauna is from the *Plesiadapis rex* zone, and authors since Dorr (1958) have considered *T. transitus* a junior synonym of *P. grangeri* (e. g., West, 1976), a view that I also hold.

The middle Tiffanian Judson locality in the Williston Basin has produced a single specimen of *Phenacodus* (SMM P77.7.154; Holtzman, 1978), which matches *Phenacodus grangeri* in size and morphology.

Gazin (1956a) described a few specimens from the Bison Basin as "*Phenacodus*? sp. (large)" (p. 46). Several additional specimens of this taxon have been collected, and these make identification as *Phenacodus grangeri* possible. The taxon is restricted to middle Tiffanian Bison Basin localities.

A lower molar from Big Bend National Park (TMM-TAMU 41274–2) matches *P. grangeri* in size. Schiebout (1974) and Rapp et al. (1983) claimed that the age of this locality is late Torrejonian or early Tiffanian (Schiebout, 1974; Rapp et al., 1983), and the specimen could be the oldest reported *P. grangeri.* Archibald et al. (1987) consider this locality *Plesiadapis rex* zone, and this is more consistent with the recovery of *P. grangeri.*

Phenacodus grangeri evolved towards larger body sizes: specimens from the *Plesiadapis rex* zone are smaller than those from the *P. simonsi* zone (Fig. 30). Clarkforkian *P. intermedius* is larger than *P. grangeri.* Wasatchian *P. intermedius* is comparable in size to late Tiffanian *P. grangeri.*

Referred specimens.—Williston Basin, *Plesiadapis rex* zone: SMM P 77.7.154 (not seen). Powder River Basin, Tiffanian: CCM 73–7, YPM-PU 20367. Bighorn Basin, *Plesiadapis rex* zone: UM 63095, 63104, 63109, 64395, 64505, 64509, 64526, 64558, 82096, YPM-PU 14854, 14858, 14860, 14979, 17772, 17776, 17777, 19464, 19465, 19561, 19563, 19582, 19584, 19585, 19594, 19610, 19914, 19915, 19924, 19928, 19937, 19941, 19960, 19973, 19978, 20015, 20030, 20081, 20254, 20290, 20306, 20313, 20343, 20549, 20625, 20626, 20629, 20636, 20642, 20772, 20775, 20836, 20883, 20885, 20894, 21243, 21257, 21292, 21293, 21427, 23947–23949, and YPM-PU field number 101–72; *Plesiadapis churchilli* zone: UM 77153, YPM-PU 17739 (in part), 17763, 17820, 17824, and 20390; *Plesiadapis simonsi* zone: UM 66214, 67266, 67267, 68251, 68252, 68254, 68787, 68791, 68799, 69253, 71326, 73515, 73516, 73588, 73600, 73663, 73673, 73689, 73690, 73693, 73979, 73982, 92283, YPM-PU 17295, 17817, 17834, 17904, 17905, 17917, 17946, 17947, 17954, 17955, 17987, 18135, 18333, 18335, 18336, 18742, 18913, 18924, 18929, 18992, 18946, 18947, 18953, 18957, 18963, 18969, 19002, 19039, 19040, 19083, 19114–19116, 19136, 19141, 20166, 20261, 20274, 20281, 20282, 20302, 20308, 20311, 20322, 20324, 20332, 20359, 20363, 20364, 20369, 20370, 20376, 20377, 20379, 20383, 20389, 20407, 23691, 23692, 23695, 23696, and 23946; Tiffanian: UM 82017, UW 13018, 13338, YPM-PU 14994, 17748, 17750, 17950, 18343, 14993, 18953, 19094, 19098, 19119, 19128, 23689, and 23699. Wind River Basin, *Plesiadapis rex* zone: AMNH 88187–88189, and 89692–89694; *Plesiadapis churchilli* zone: CM 12460, 12462, 12467, 12468, 12475, 16208, 16212, 16216, 16217, 23770–23777, and 23782; Tiffanian: UCM 42007 and 42008. Fossil Basin, *Plesiadapis rex* zone: UM 83898, 85679, USNM 21265–21267, and 406123–406127. Green River Basin, *Plesiadapis rex* zone: UM 34762 (Holotype *T. transitus*), 34781, 34782, 55120, 55121, 68378, 69546, 74007, 80797, 80808, 83653, 87791, USNM 214541, and USNM accession number 59–64 (in part). Bison Basin, *Plesiadapis rex* zone: UCM 40471, UCMP 111967, and USNM 21038; *Plesiadapis simonsi* zone: UW 1091; Tiffanian: USNM 21025. Washakie Basin, *Plesiadapis churchilli* zone: UW 13237; *Plesiadapis simonsi* zone: UW 13241. San Juan Basin, Tiffanian: AMNH 17186–17189, 17192, 17196, 17198, 56278, 56282, 56291, UM 71351, USNM 10642 (in part), and 10645. Big Bend National Park, *Plesiadapis praecursor* zone: TMM-TAMU 41274–2 and 41274–3; *Plesiadapis rex* zone: TMM-TAMU 41048–10, 41048–13, 40148–23, 40642–1, 41273–1, 41366–11, 41366–12, 41366–29, 41366–35–40, 41366–49, 41366–60, 41366–61, 41366–63, 41366–67, 41366–69, 41366–72, and 41368–1; Tiffanian: TMM-TAMU 41047–19 (in part).

Phenacodus magnus, new species
Fig. 37

Phenacodus primaevus (in part), West, 1976, p. 33; Holtzman, 1978, p. 58; Winterfeld, 1982, p. 100.

Holotype.—YPM-PU 21065, right C_1, and P_4-M_2, left P_1 and P_2 fragments, right P^4-M^2, two incisors, and numerous bone fragments. The specimen comes from a locality of the *Plesiadapis simonsi* zone of the Clarks Fork Basin (680 m in the Clarks Fork Basin section, Sec. 14, T57N, R100W).

Age and distribution.—*Plesiadapis churchilli* and *P. simonsi* zone of the Tiffanian from Williston, Bighorn, Wind River, Washakie, and San Juan Basins.

Diagnosis.—Size similar to *P. trilobatus,* larger than other phenacodontids. Differs from *P. trilobatus* by the narrow trigonid basin of P_4 and the short trigonid basin of the molars. P^4 short and with large parastyle unlike *P. trilobatus.*

Description.—The holotype is the most complete dentition for any specimen of *P. magnus,* P_3-M_3 and P^4-M^3 are also known from other specimens. *P. magnus* differs mainly in size from *P. grangeri,* although some minor differences in shape occur (see discussion of *P. grangeri*). *P. magnus* is similar in size to Wasatchian *P. trilobatus.* A possible shape difference is the narrow trigonid basin of P_4 in *P. magnus.* The ratio (distance protoconid-metaconid)/(length) of P_4 is 0.23 in *P. magnus* (N = 2), and 0.29 in *P. trilobatus* (N = 8; SD = 0.03). In addition, the trigonid basin of M_1 and M_2 is shorter in *P. magnus* than in *P. trilobatus,* which is possibly the result of the reduced paraconid and paracristid. The parastyle of P^4 is usually large in *P. magnus.* P^4 is comparable in width to *P. grangeri,* but wider than in *P. trilobatus* (Table 5).

Discussion.—Two specimens of a large phenacodontid have been found at the Tiffanian Riverdale locality of the Williston Basin. FMNH.P 8661 is a D^4 which is larger than all known D^4s of *Phenacodus grangeri.* It seems likely that this specimen represents *P. magnus.* A second specimen from the same locality (FMNH.P 8662), is a nondiagnostic fragment of an upper molar, here tentatively referred to the same taxon. These specimens corroborate the tentative age estimate of Riverdale cited by Archibald et al. (1987): *Plesiadapis churchilli* zone. *P. magnus* is also known from the Medicine Rocks: YPM-PU 16569 from 7-UP Butte, and YPM-PU 20366 from White Site. These specimens indicate that the Medicine Rocks localities yield fossils from the *Plesiadapis churchilli* zone. Archibald et al. (1987) suggested that these localities produce fossils from the *Plesiadapis anceps* zone.

A deformed specimen that is possibly *P. magnus* (YPM-PU 19133) was, according to its label, found "WSW of Sage Point" in the Clarks Fork Basin, and is apparently from the same locality as two specimens of *Ectocion cedrus* and a specimen of *P. grangeri* with similar locality information. The color of the fossil bone is white in the specimen of *P. magnus,* unlike typical fossils from Clarks Fork Basin mudstones, which are black. This may indicate that the specimen did not come from a mudstone, but from a sandstone or conglomerate. The specimen may be a diagenetically expanded specimen of *P. grangeri.*

Two specimens of *Phenacodus magnus* are known from the locality Seaboard Well in the northern Clarks Fork Basin (YPM-PU 20386 and 20387). Archibald et al. (1987) suggested that the Seaboard Well yields a fauna from the *Plesiadapis rex* zone, but the occurrence of *Phenacodus magnus* at this locality might indicate that it is in the *Plesiadapis churchilli* zone.

A few specimens of *P. magnus* are known from Malcolm's locality in the Wind River Basin (CM 12465 and 12466). The taxon is associated with *P. grangeri* at this locality. *Phenacodus magnus* is also known from the Washakie Basin (UW 13238). Occurrence of this taxon is consistent with the age of the locality proposed by Winterfeld (1982): *Plesiadapis churchilli* zone.

Two *Phenacodus* specimens from the Tiffany fauna of the San Juan Basin are here referred to *P. magnus* (AMNH 56279 and 56286). These specimens were collected after Simpson's publications on the fauna (1935b, c).

Referred specimens.—Powder River Basin, *Plesiadapis churchilli* zone(?): YPM-PU 16569 and 20366. Williston Basin, *Plesiadapis churchilli* zone: FMNH.P 8661 and P 8662. Bighorn Basin, *Plesiadapis churchilli* zone: UM 71319, 77198, 80582, 80667, 83218, 85930, 91319, YPM-PU 14859, 14966, 14973, 14975, 17737, 17739 (in part), 17740, 17747, 17815, 18112, 19133(?), 20386, and 20387; *Plesiadapis simonsi* zone: UM 73992, 74028, 74037, 77304, 77305, 80357, 83564, 92146, 92358, YPM-PU 17875, 18292, 18730, 18916, 18962, 19140, 19162, and 20279; Tiffanian: UM 92422, and YPM-PU 19874. Wind River Basin, *Plesiadapis churchilli* zone: CM 12465 and 12466. Washakie Basin, *Plesiadapis churchilli* zone: UW 13238. San Juan Basin, Tiffanian: AMNH 56279 and 56286.

Phenacodus vortmani (Cope, 1880)
Fig. 38

Hyracotherium vortmani Cope, 1880, p. 747.
Phenacodus apternus Cope, 1882a, p. 180.
Phenacodus wortmani, Cope, 1882a, p. 179.
Phenacodus vortmani, Cope, 1882f, p. 199; Cope, 1885, p. 464, pl. 57g-h, 58:8–10; Granger, 1915, p. 343, fig. 6 and 8; Kelley and Wood, 1954, p. 350, fig. 7c; Robinson, 1966, p. 53, pl. 10:6; Guthrie, 1967, p. 40; Delson, 1971, p. 345, fig. 21; West, 1971, p. 16, fig. 11; West, 1973, p. 137, fig. 13b-c; Bown, 1979, p. 99, fig. 55a-c; Davidson, 1987, p. 114.
Phenacodus copei Granger, 1915, p. 344, fig. 5 and 7; Kelley and Wood, 1954, p. 349, fig. 7b.
Phenacodus almiensis Gazin, 1942, p. 219, fig. 2; Gazin, 1956c, p. 13, pl. 2:3–4; West, 1971, p. 14, fig. 8a-b.
Phenacodus copei?, Dorr, 1958, p. 1228.
Phenacodus cf. *vortmani,* Gazin, 1962, p. 66, fig. 8–9.
Phenacodus matthewi, McKenna, 1960, p. 97, fig. 51–52.
Phenacodus vortmani (in part), Guthrie, 1971, p. 81; Rose, 1981, p. 71, pl. 2.1, 3.1, and 3.2.
Phenacodus sp. (in part), Rose, 1981, p. 73.
Phenacodus bisonensis (in part), Winterfeld, 1982, p. 99.
Phenacodus cf. *P. intermedius,* Gingerich, 1989, p. 52, fig. 34.

A

B

0   5mm

C

D

E

F
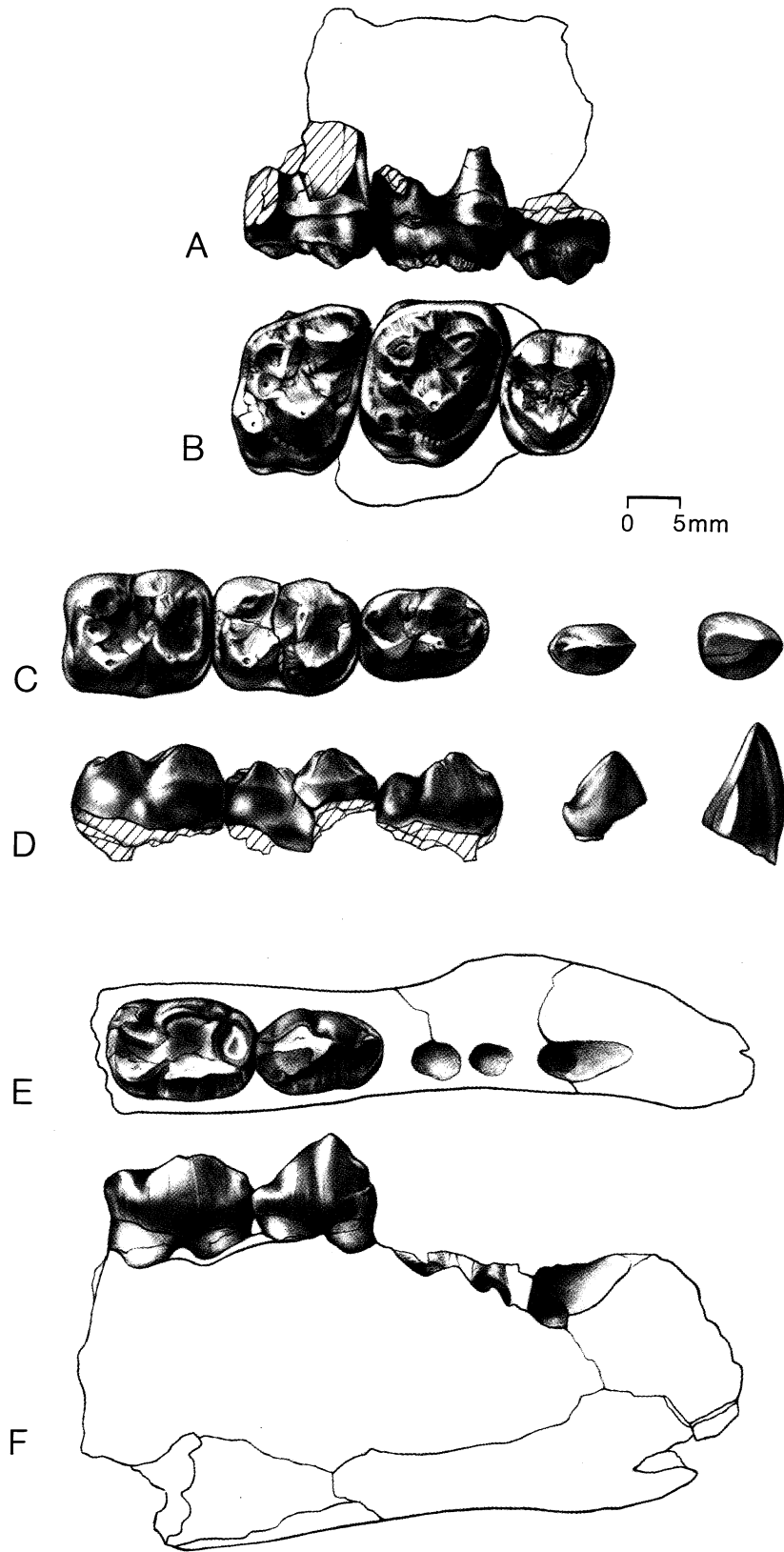
Holotype.—AMNH 4824, left dentary with P_4 and fragment of M_1, roots for P_3 and M_3, and alveoli for P_{1-2}, from "Lost Cabin Beds, Alkali Creek, Wind River Basin" (Granger, 1915). The specimen is *Lambdotherium* zone in age.

Age and distribution.—*Plesiadapis churchilli* zone of the Tiffanian through *Palaeosyops* zone of the Bridgerian from the Powder River, Bighorn, Wind River, Green River, Fossil, Great Divide, Washakie, Sand Wash, Laramie, Shirley, Piceance, Huerfano, and San Juan Basins.

Diagnosis.—Similar in size to *P. bisonensis*, smaller than *P. intermedius*. M_2 and M_3 narrower, M_2 shorter than other Wasatchian *Phenacodus*. Differs from *P. bisonensis* in the wider P_4 trigonid basin and common absence of the P_4 entoconid. P^4 metaconule usually absent, unlike *P. bisonensis*.

Description.—A partial skull and skeleton of *P. vortmani* (AMNH 4378) were described by Cope (1885). The complete adult dentition, except I_3, is preserved in this specimen. Additional skulls of *P. vortmani* are known: one specimen will be described below (YPM 20524), and there is an undescribed specimen in Carnegie Museum. UM 83570 is a partial skull of a young individual. Fragmentary skeletons are included in AMNH 4378 as well as in the holotype of junior synonym *P. almiensis* (USNM 16691). West (1971) described the deciduous dentition.

The Buckman Hollow specimens of *P. vortmani* have often been referred to *P. almiensis*. One morphological difference between the Buckman Hollow sample and other *P. vortmani* is the large mean height of the mesostyle of M^2 (N=3; mean=1.6 mm; SD=0.06) compared to Tiffanian and Clarkforkian *P. vortmani* from the Bighorn Basin (N=6; mean=0.9; SD=0.4). The coefficient of variation of this measure is large, and the character does not distinguish adequately between *P. almiensis* and *P. vortmani*.

Phenacodus vortmani is smaller than *Phenacodus intermedius*, although identification of fragmentary specimens is sometimes impossible. The size difference is usually clear in the middle to late Wasatchian (central Bighorn Basin Section), but is less apparent in Tiffanian, Clarkforkian and early Wasatchian zones. The Wasatchian taxa referred to *Phenacodus* are best distinguished on the basis of the scores on principal component 1 (a measure of size here) in an analysis of length and trigonid width of M_{1-2} (Fig. 35). Two specimens here referred to *Phenacodus vortmani* on the basis of their score on PC-1 are particularly ambiguous. A dentary with P_2-M_3 and isolated P^3 (UM 64969) is the largest Wasatchian *P. vortmani* and the outlier at the 1600 m level of the Clarks Fork Basin section. P_4 and M_1 of this specimen are of moderate size, but M_2 is
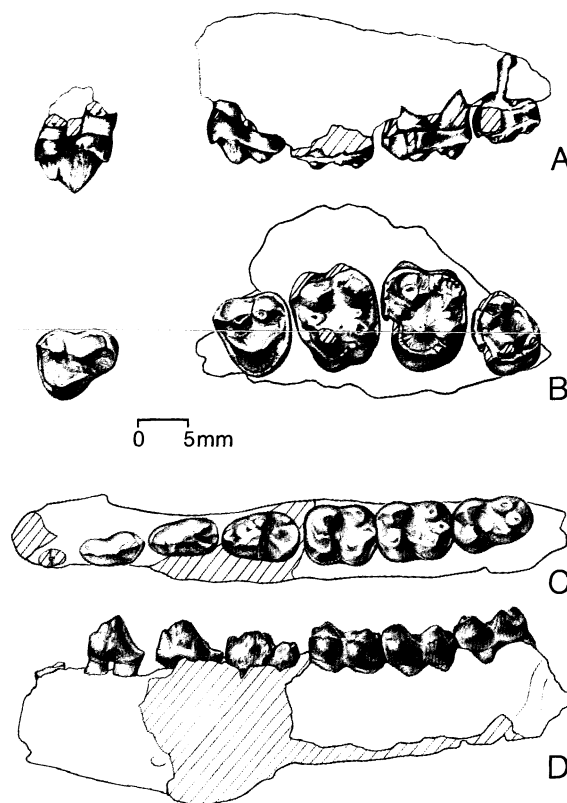
Figure 38. Dentition of early Wasatchian *Phenacodus vortmani* from Clarks Fork Basin. A and B, right P^3, left P^4-M^3 (UM 76474) in labial and occlusal view, Lower *Haplomylus-Ectocion* zone. C and D, P_2-M_3 (UM 66251) in occlusal and labial view, Lower *Haplomylus-Ectocion* zone.

large (Figs. 33 and 34). Another outlier is from the *Cantius torresi* zone (1520 m), consisting of a dentary with P_4-M_3 (UM 83622). This specimen has a P_4 that is larger than any other *P. vortmani*, and similar is size to *P. intermedius*. Unambiguous identification of a specimen of *Phenacodus* is only possible when specimens are relatively complete, or large homogeneous samples are available.

Discussion.—Cope (1880) established *Hyracotherium vortmani* for the holotype (AMNH 4824). Subsequently he (1881a) referred the taxon to *Phenacodus* and changed "vortmani" to "wortmani." Although the correct generic name was first associated with "wortmani," and although the taxon was named for J. L. Wortman, the spelling of 1880 has priority and to be retained: *Phenacodus vortmani*.

Phenacodus apternus, Cope 1882a, was distinguished from *P. vortmani* on the basis of the outline of M_3. As pointed by Granger (1915), this character is variable and not different between the type samples of *P. vortmani* and

Figure 37. Dentition of *Phenacodus magnus*. A and B, P^4-M^2 of holotype (YPM-PU 21065) from Clarks Fork Basin in labial and occlusal view. C and D, C_1, P_2, P_4-M_2 of holotype (YPM-PU 21065) in occlusal and labial view. E and F, P_{3-4} (UM 83218) from Divide Quarry in occlusal and labial view.

P. apternus. Granger (1915) established *P. copei* for a number of small specimens here referred to *P. vortmani.* Granger described differences in morphology and size, and also noted a specimen from the Bighorn Basin that combined the morphological characters of the two taxa. Guthrie (1967) discussed the synonymy of *P. vortmani* and *P. copei,* and was followed in this by later authors.

Gazin (1942, 1956c) described a number of *Phenacodus* specimens from the Green River Basin as *P. almiensis.* He did not compare the taxon to *P. vortmani,* but noted differences between *P. almiensis* and *P. copei* (Gazin, 1956c): *P. almiensis* is larger, its P^3 has stronger protocone and conules, P^4 is molariform, and the upper molars have stronger preprotocrista and postprotocrista. These morphological differences between Bighorn Basin *P. vortmani* and the type collection of *P. almiensis* are not apparent based on the larger samples now available. The most impressive difference in Gazin's view was size. Some size decrease occurs in the *P. vortmani* lineage (Figs. 32–35), but the *P. almiensis* sample is not different in size from the late Tiffanian and Clarkforkian *P. vortmani* sample of the Bighorn Basin. A morphological difference between the Buckman Hollow and Bighorn Basin samples is the size of the mesostyle, as pointed out above. Until further material becomes available I follow West (1976) in synonymizing *P. almiensis* with *P. vortmani.*

The ambiguity of the distinction between *P. vortmani* and *P. intermedius* has not led any author to synonymize the two taxa. The main reasons to recognize two taxa are the bimodal size distribution and the absolute difference between the modes, as well as the pattern of distribution of taxa through stratigraphic sections. *Phenacodus vortmani* is nearly absent in the Upper *Haplomylus-Ectocion* zone, while *Phenacodus intermedius* is common in the lower part of that zone. *P. vortmani* is abundant in the *Bunophorus* and *Heptodon* zones, where *P. intermedius* is virtually absent. *P. vortmani* is larger than *Copecion brachypternus.* Shape differences are listed in Table 6 and are discussed in the section on *C. brachypternus.*

Evolution in *Phenacodus vortmani* includes a decrease in size. Late Tiffanian and early Clarkforkian specimens are larger than middle and late Clarkforkian specimens (Figs. 32–35). Guthrie's (1967) conclusion that *P. vortmani* from the *Lambdotherium* zone is smaller than *P. vortmani* from the *Heptodon* zone is not apparent, although P_3 and P_4 of *P. vortmani* from the *Heptodon* and *Lambdotherium* zone of the Wind River Basin are significantly smaller than those from the earlier Wasatchian of the Bighorn Basin.

P. vortmani was not known from the Upper *Haplomylus-Ectocion* zone when Schankler discussed faunal evolution in the Bighorn Basin (1980, 1981), but 3 specimens are now known between levels 245 m and 296 m of the central Bighorn Basin section (USGS 9003, 13717, and an M^3 catalogued as part of YPM 36022). *Phenacodus vortmani*

Table 6. Ratios of cheek teeth of *Phenacodus vortmani* and *Copecion brachypternus.*

	P. vortmani			C. brachypternus		
	N	Mean	SD	N	Mean	SD
P^3W/L	22	0.94	0.08	8	0.80	0.08
P_3W/L	87	0.59	0.04	32	0.52	0.04
P_4W/L	186	0.68	0.05	61	0.61	0.04
P_4Wtrb/L	39	.025	0.05	11	0.19	0.06
M_1L/P_3L	36	1.10	0.08	18	0.94	0.07

is abundant in the *Heptodon* zone of the Bighorn Basin and its last occurrence is at the 690 m level of the central Bighorn Basin section. The taxon is also known from the *Heptodon* through *Palaeosyops* zones of the Wind River Basin (Kelley and Wood, 1954; Guthrie, 1967 and 1971), and from localities in the Indian Meadows Formation near the Boysen Reservoir (UW 14858, 14859, and 17349).

Specimens of *P. vortmani* from the Washakie Basin near the Rock Springs uplift were originally reported as *P. bisonensis* (Winterfeld, 1982). A P^4 in the sample (UW 13308) resembles *P. vortmani* in the lack of a metaconule, which is consistent with the suggested late Tiffanian age of the fauna. McKenna (1960) reported two specimens of *Phenacodus matthewi* from the Wasatchian Four Mile Fauna. The three specimens now available are within the size range for *Phenacodus vortmani,* although all three are smaller than average. I refer these specimens to *P. vortmani.* Davidson (1987) described *P. vortmani* from the Cooper Creek Fauna of the Laramie Basin. No adequate age control is available for a specimen of *Phenacodus vortmani* from the Shirley Basin (UW 2161), although *Hyrachyus* and *Brontops* were recovered at nearby localities in the same formation. The latter two taxa are characteristic of Bridgerian faunas and would indicate that the Shirley Basin specimen is the youngest record of *P. vortmani* if found at the locality of UW 2161. Reeside (1924) identified three specimens from two localities in the Tiffany area of the San Juan Basin as "*Tetraclaenodon*" and "*Tetraclaenodon* or *Phenacodus*" (p. 47). These specimens lack the teeth that best diagnose the two genera, but morphological and age information is most consistent with identification as *Phenacodus vortmani.*

Referred specimens.—Powder River Basin, Lower *Haplomylus-Ectocion* zone: AMNH 56186, 56328, UCM 52466, USNM accession number 52–61AC, and UW 6787. Bighorn Basin, *Plesiadapis churchilli* zone: UM 71703; *Plesiadapis simonsi* zone: UM 68797, 71417, 71709, 73579, 73659, 73672, 73983, 73985, YPM-PU 17917, 17953, 17976, 18915, 18939, 18944, 18952, 18957, 19167, 20283, 20309, and 20365; *Plesiadapis gingerichi* zone: UM 68733, 68884, 69928, 71300, 71302, 71793, 71819, 73337, 77157, YPM-PU 18998, 18928 (in part), and 19004; *Plesiadapis cookei* zone: UM 66150, 66628, 66922, 71641, 80261, 91465, YPM-PU 20118, 20169 (in part), and 20260; *Phenacodus-Ectocion* zone: UM 64714, 65668, 66288, 66304, 66305, 66310, 66574, 66585, 66587, 67242, 67443, 68220, 69333, 83200, 83426, and 83796;

Cantius torresi zone: UM 77203, 83570, 83618 (in part), 83622, 83636, and 87354; Lower *Haplomylus-Ectocion* zone: UM 63822, 64696, 64788, 64969, 64987, 65394, 66251, 66283, 66363, 66478, 67362, 68108, 68131, 68724, 69457, 71061, 72906, 72914, 73853, 75929, 76034, 76035, 76213, 76474, 77056, 80308, 80319, 80408, 80762, 82741, 86974, 87075, 87280, 87326, 87480, 88024, 88040, USGS 5036, 6989, 9097, 9697, 10499, 19220, 19315, UW 7451, 7459, 7462, 7467, 7468, 9275, 9278, 9279, 9282, 10396, YPM 19047, 21641, 23678, 25413, 32538, 32551, 32605, 33141, 34398, 35975, 35987, 35993, 36002, 36030, 36678, 36695, 36706, 37821, 37823, and YPM-PU 16146; Upper *Haplomylus-Ectocion* zone: UM 85690, USGS 8017, 9003, 13717, and YPM 36022 (in part); *Bunophorus* zone: UM 64344, 75286, 91214, 91219, 91226, 91227, 91243, 91265, 91751, 91778, 91798, USGS 700, 705, 1326, 1346, 1347, 4316, 4317, 4322–4332, 4334, 4335, 4370–4372, 4377–4384, 4406, 4420, 5152, 7127, 7309, 7347, 7920, 7957, 8243, 8289, 8429, 8570, 8766, 8805, 8855, 8957, 9342, 9393, 9447, 9448, 9684, 9705, 9715, 9789, 9790, 9798, 10162, 10163, 10180, 10189, 10202, 10210, 10211, 10218, 10220, 10221, 12234, 17849, 17851, 17852, 17874, 17875, 17877, 18286, 18287, 18296, 18297, 18302, 18303, 18304, 18307–18309, 18311–18318, 18327, 19208, 19214, 19272, 19273, 19284–19287, 19297, 19307, 19308, YPM 22993, 26530, 26580, 26655, 26808, 27099, 36667, 37803, 37826, and 37851; *Heptodon* zone: UM 75480, 75497, 86605, 87961, 88116, 88254, 88255, 91013, 91133, 91138, 91171, 91340, 91456, 91461, 91537, 91584, 91644, 91676, 91709, 91711, 92050, 92053, 92063, 92081, 92162, USGS 694–697, 699, 700, 704, 725, 812, 853, 963, 965–967, 977, 978, 980–982, 1078–1082, 1199, 1287, 1300, 1333, 1540–1542, 1552, 1572, 1573, 1603, 1604, 1638, 1700–1702, 1747, 1795–1797, 1941, 3549, 3587, 3659, 3667, 4336, 4337, 4351, 4352, 4358, 4403–4405, 4417–4419, 4421, 5038, 5110, 5112–5115, 5155, 5367, 6114, 6329, 6330, 7012, 7041, 7054, 7250, 7292, 7339, 7647, 7707, 7861, 7893, 7894, 7958, 7967, 8009, 8035, 8036, 8072, 8132, 8230, 8260, 8283, 8297, 8307, 8356, 8366, 8381, 8398, 8399, 8488–8491, 8533, 8607, 8664, 8686, 8692, 8694, 8697, 8715, 8722, 8758, 8814, 8845, 8855, 8859, 8894, 8935, 9050, 9064, 9239, 9242, 9275, 9541, 10164, 10166, 10170, 10172, 10177, 10184, 10185, 10187, 10197, 10200, 10214, 10482, 12234, 13756, 13783, 17880, 17881, 18305, 18306, 19211, 19213, 19215, 19271, 19276, 19281, 19282, 19304, YPM 17578, 17679, 17685–17689, 17693, 17694, 17695, 17699, 17954, 18631, 18632, 18634, 18768, 18892, 18894, 18895, 18897, 18908, 20524, 22798, 22974, 22976, 22979, 22981, 22982, 22984, 22987, 22992–22997, 23598, 26584, 27442, 27460, 27461, 27470, 27507, 27519, 27667, 27676, 27693, 28016, 28713, 28811, 28838, 28879, 29516, 29819, 33928, 34969, 35218, 35267, 35963, 35964, 35966, 35997, 36006, 36009, 36029, 36660, 36676, 37799–37802, 37806–37808, 37810–37820, 37828, 37829, 41423, and 41424; *Lambdotherium* zone: USGS 7582, 10213, 16466, 17862, 26655, YPM 23008, and 37824; Wasatchian: AMNH 15333, 15336, 15772, 4378 (holotype *P. copei*), 4380, UM 63897, 63914, 67567, 75206, 75529, 76152, 85254, 87221, 87987, 91214, USGS 698, 7032, 7033, 7905, 7999, 8185, 8336, 8811, 10175, 10183, 11174, 17699, 17856, 17858, 17951, 18974, 19207, 19210, 19274, 19275, 19283, 19365, 19367, YPM 22983, 22989, 25423, 26247, 26860, 27182, 32581, 32582, 33124, 35977, 36003, 36659, 36668, 36679, 38043, and 38087–38089. North Fork of Shoshone River, *Lambdotherium* zone: UM 80843 and 80845. Wind River Basin, Clarkforkian: AMNH 86843 (in part); *Heptodon* zone: ACM 336, 3531, 10121, 11222, 11241, AMNH 12784–12787, 12789, 12790, 14800, 93129, CM 19856, 19857, 22663, 22665, 22668, 22669, 22671, 28717, 28930, 37075, 39496, MCZ 20335, 30336, YPM-PU 16204, 20140, 20464, 20465, USNM 187458, 187459, and 187464; *Lambdotherium* zone: AMNH 2983, 4825–4827, 14787, 14797, 14799, 14801, 93127, 93131, CM 34874, 43396, MCZ 3490, UCM 44455, 46735, 47023, USNM 187431, 187498, 187504, 187507, 187508, UW 17343, YPM-PU 13438, 13441, and 20137; *Palaeosyops* zone: CM 44816; Wasatchian: MCZ 20335, USNM 187426, UW 12381, 14857–14859, 17338, 17340, 17342, 17344, 17345, and 17347–17349; Fossil Basin, Wasatchian: USNM 22433. Green River Basin, Clarkforkian?: CM 8871, UM 68359, 68362, 68364, 68370, 71329, 71341, 79854, USNM 16691 (holotype *P. almiensis*), 16692–16694, 20637–20639, 20641–

20643, 20650–20654, 21286, 26326, 26327, 406156–406169, 409471, 409475, and USNM field number 29–61A; *Lambdotherium* zone: FMNH.PM 15508, 15510, 15605, and 15956. Great Divide Basin: UW 5752. Laramie Basin, Wasatchian: UW 2946, 10025, 10050, 10506, and 20221. Washakie Basin, *Plesiadapis simonsi* zone: UW 13308 and 13324. *Plesiadapis cookei* zone: UCMP 133840; Lower *Haplomylus-Ectocion* zone: AMNH 80107, UCM 29026, UCMP 44034 and 46168. Shirley Basin, Wasatchian?: UW 2161. Piceance Basin, Clarkforkian: FMNH.PM 222, P 15532, 15566, 15587, 26114, 26126, 26127, UCM 41057, 41292, and 48643; *Lambdotherium* zone: FMNH.PM 254; Wasatchian: FMNH.P 26735. Huerfano Basin, *Heptodon* zone: AMNH 55230 and 56522; *Lambdotherium* zone: AMNH 17547, 55229, 55276, and 55278–55280. San Juan Basin, *Heptodon* zone: AMNH 16248, 16251, 16252, 48758, 80678, 80696, CM 49468, 49470, and 49474–49476; Tiffanian: USNM 10640, 10642 (in part), and 10649.

Phenacodus intermedius Granger, 1915
Fig. 39

Phenacodus intermedius Granger, 1915, p. 340, figs. 35, 37, and 39.
Phenacodus primaevus, Simpson, 1937c, p. 17; Gazin, 1956c, p. 15, pl. 2.5; West and Atkins, 1970, p. 2, fig. 1; Delson, 1971, p. 345; West, 1973, p. 137, fig. 13d; Rose, 1981, p. 71, pl. 2.2 and 3.3; Princhinello, 1971, p. 84, fig. 6c.
Phenacodus primaevus (in part), Guthrie, 1971, p. 81; West, 1976, p. 33, fig. 21; Bown, 1979, p. 97, fig. 54d-e; Davidson, 1987, p. 114.
Phenacodus privaevus hemiconus, Dorr, 1958, p. 1228.
Phenacodus intermedius, McKenna, 1960, p. 99.
Phenacodus cf. *P. primaevus*, Wilson, 1967, p. 165, fig. 116.

Holotype.—AMNH 15761, right dentary with P_4-M_3, left dentary with P_3-M_2, M_3 fragment, palate with right P^4-M^2, left M^{2-3}, from "Gray Bull Beds, Five Mile Creek, Bighorn Basin" (Granger, 1915:340). Granger's fieldbook of 1911 indicates that the specimen was collected on July, 1 on the south side of the creek. On the same day Granger's field team collected a specimen of *Arfia opisthotoma* in the same area (J. Alexander, pers. comm., 1989). This suggests that the holotype of *P. intermedius* is from the Lower or Upper *Haplomylus-Ectocion* zone.

Age and distribution.—Clarkforkian through Bridgerian of the Powder River, Bighorn, Wind River, Green River, Washakie, Laramie, Piceance, Huerfano, and San Juan Basins, and Big Bend National Park.

Diagnosis.—Similar in size than *P. grangeri*. Larger than contemporaneous *P. vortmani* and smaller than contemporaneous *P. trilobatus*. P^4 often equally wide as long, unlike *P. grangeri*.

Description.—All permanent teeth except I_1 are known for *P. intermedius*, as well as D_{2-4} and D^{3-4}. West (1971) described the deciduous dentition. A skull and skeleton of *Phenacodus intermedius* was described by Cope (1885) as *P. primaevus*, and an endocast was described by Cope (1882d) and Simpson (1933). Another skull from the paleontology exhibit of Princeton University (PU 14864) will be described below. The specimen consists of a skull and postcranial skeleton, and the whole adult dentition except I_1. The label records: "Channel ss, 20 mi. W. of Basin, 1.5 mi. S. side Elk Creek, Bighorn Co., Wyo." This locality information indicates that the specimen is from the *Bunophorus* zone or later Wasatchian.
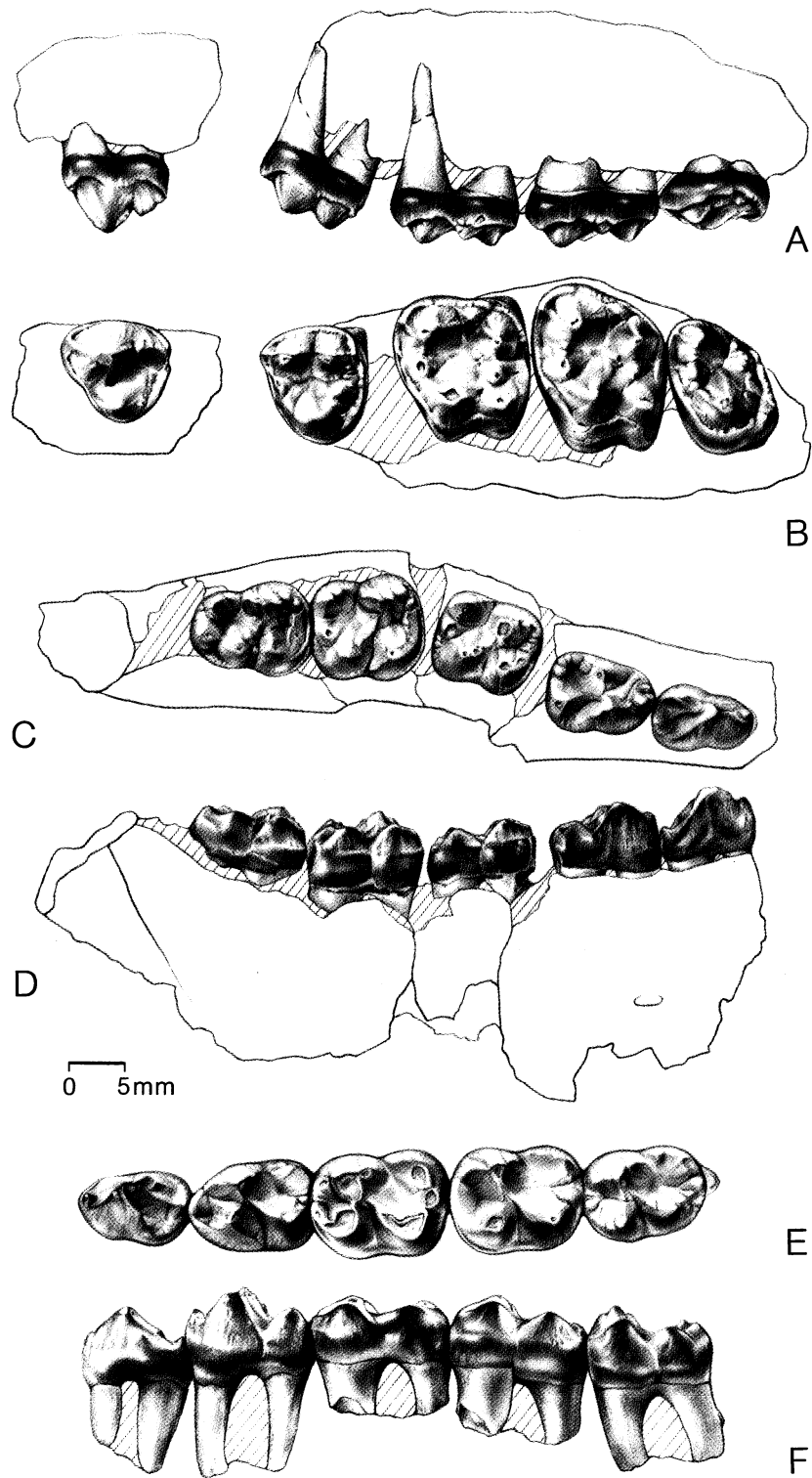
Figure 39. Dentition of *Phenacodus intermedius* from Clarks Fork Basin. A and B, P^3-M^3 (UM 83619) in labial and occlusal view, *Phenacodus-Ectocion* zone. C and D, P$_3$-M$_3$ (UM 69947), occlusal and labial view, Upper *Haplomylus-Ectocion* zone. E and F, P$_3$-M$_3$ (UM 73721), occlusal and labial view, *Plesiadapis gingerichi* zone.

I$_2$ of PU 14864 has a spatulate, well worn crown which projects medially near the occlusal edge. The posterior side bulges near the enamel-dentin boundary. I$_2$ has posteriorly an interdental wear facet for I$_3$, but no such facet for I$_1$ is present. I$_3$ is similar in shape to I$_2$, but more asymmetrical.

The lower canine is strongly curved and triangular in cross section. The surface of the enamel bears low longitudinal ridges and furrows, but it is smoother than the canine of *Ectocion*. The canine is separated from I$_3$ and P$_1$ by a diastema.

P$_1$ has one root and a pointed tip. P$_2$ is double rooted and has a weak lingual and strong posterior cingulum, but lacks the talonid basin. A weak crest extends anteriorly and two crests extend posteriorly from the protoconid. Diastemata occur on either side of P$_2$.

Left and right I^1 are separated by a diastema. Both teeth are damaged, but probably resemble I^2. I^2 has a low crown and pointed tip and is heavily worn. I^3 of PU 14864 has a high crown and is pointed. Diastemata occur between the upper incisors and on either side of the upper canine.

The upper canine is less curved, but longer anteroposteriorly and narrower mediolaterally than the lower canine. It is oval in cross section. P^1 is single rooted and its tip is more pointed than I^3 and P$_1$. P^2 is double rooted and has a lingual cingulum. It is broadened posteriorly and the protocone is absent. A crest extends from the paracone anteriorly and posteriorly.

P^4 of *P. intermedius* is approximately equally wide as long, and can be used to distinguish between *P. intermedius* and *P. grangeri* (Table 5). In addition to this, *Phenacodus grangeri* is smaller than Clarkforkian *P. intermedius*, but late Tiffanian *P. grangeri* is similar in size to Wasatchian *P. intermedius*. A single astragalus known for *P. grangeri* (YPM-PU 19594) has a broader sustentacular facet than the astragalus of *P. intermedius*.

Discussion.—Granger (1915) distinguished *P. intermedius* from the different "subspecies" of larger contemporaneous *Phenacodus* on the basis of size, details of dental morphology, and a short skull. Study of the present large sample indicates that the morphological differences are not consistent between the taxa and that size is the only character that separates *P. intermedius* from large contemporaneous *P. trilobatus*. West (1976) noted that the two taxa were morphologically indistinguishable, and considered the size difference too small to merit recognition of two taxa. Based on a large sample with adequate stratigraphic data, Schankler (1981) followed Granger (1915), Simpson (1937c) and Guthrie (1971) in recognizing two taxa. According to Schankler (1981), variation in large Wasatchian *Phenacodus* at any one stratigraphic level (or time plane) is too large to be attributed to a single species. Moreover, at different Wasatchian levels smaller or larger specimens dominate. Smaller specimens are particularly abundant in the Lower *Haplomylus-Ectocion* zone, larger individuals dominate in the later half of the Upper *Haplomylus-Ectocion* zone (Figs. 32 to 35). This distribution makes it is

unlikely that larger and smaller individuals represent the two sexes of a single taxon. It is also unlikely that the larger mean size of specimens from the Upper *Haplomylus-Ectocion* zone is the result of anagenetic size increase from specimens from the Lower *Haplomylus-Ectocion* zone, because large specimens have been found in early Wasatchian deposits. The taxa are different lineages and their relative abundance changes in the lower half of the Upper *Haplomylus-Ectocion* zone.

Phenacodus as large as *P. trilobatus* is not known from the Clarkforkian. The total size range of Clarkforkian *Phenacodus intermedius* is smaller than for combined Wasatchian *P. intermedius* and *P. trilobatus,* and the mode of the size distribution is intermediate between smaller and larger Wasatchian forms (Figs. 32 to 35). Because the mode is closer to that of the smaller Wasatchian form, I refer the Clarkforkian forms to that taxon: *Phenacodus intermedius. Phenacodus intermedius* ranges in the Bighorn Basin from the early Clarkforkian to the late Wasatchian. Evolution in the taxon includes size decrease in the early Wasatchian and possibly decrease of premolar size in the *Heptodon* zone. No linear measure distinguishes adequately between *Phenacodus intermedius* and *Phenacodus trilobatus,* but best differentiation is given by principal component 1 in a principal component analysis of length and width of trigonid and talonid of M$_1$ and M$_2$ (Fig. 38). The size distributions of *Phenacodus intermedius* and *Phenacodus trilobatus* overlap.

Phenacodus intermedius specimens are often referred to *P. primaevus.* Delson (1971) described *Phenacodus primaevus* from the early Wasatchian Powder River Local Fauna. On the basis of size, I refer these specimens to *Phenacodus intermedius.* The localities that yield the Powder River Local Fauna span a large part of a stratigraphic section published by Sharp et al. (1964), and the localities that are high in the section, such as Dry Well, may be in different biochrons. The Upper *Haplomylus-Ectocion* zone of the Bighorn Basin is characterized by its phenacodontid fauna: the absence of *Copecion brachypternus,* the virtual absence of *P. vortmani,* and the dominance *P. intermedius* over *P. trilobatus.* If the pattern of faunal evolution in the Powder River Basin resembles that in the Bighorn Basin, phenacodontids can be used to estimate the age of these faunas. Two specimens of a large *Phenacodus* from the locality Dry Well are too fragmentary for definite identification as *P. intermedius* or *P. trilobatus,* but *Copecion brachypternus* has also been found here. The combined occurrence of *Ectocion osbornianus, Copecion brachypternus,* and *Phenacodus vortmani* is consistent with an early Wasatchian (Lower *Haplomylus-Ectocion* zone) age for the localities at which these phenacodontids occur.

Simpson (1929c) and Rose (1981) reported two upper molars of *Phenacodus* (AMNH 22197, YPM-PU 17713) from the Clarkforkian Bear Creek locality in the northwestern part of the Clarks Fork Basin. I refer these to *P. intermedius.* The earliest *Phenacodus intermedius* from the Big-

horn Basin occurs at 985 m (early Clarkforkian) in the Clarks Fork Basin section. In the central Bighorn Basin, *P. intermedius* is abundant in the Lower *Haplomylus-Ectocion* zone (Bown, 1979), but rare in the Upper *Haplomylus-Ectocion* zone. It is also known from the *Heptodon* zone, and is represented by a single specimen in the *Lambdotherium* zone (YPM 36685, at 680 m in the central Bighorn Basin section). It is also known from the *Lambdotherium* zone of the North Fork of the Shoshone River.

Phenacodus intermedius is not known from the *Heptodon* zone of the Wind River Basin, but has been recovered in early Bridgerian faunas (West and Atkins, 1970; Guthrie, 1971; Krishtalka et al., 1987). *Phenacodus intermedius* is also known from the Indian Meadows Formation of the Wind River Basin, locality 13E of Keefer (1965) yielded an unnumbered specimen in the USNM collection, and UW 17335 was found near Boysen Reservoir.

Phenacodus intermedius was recovered in the Togwotee Pass area of the Wind River Basin. A P⁴ from the Second Taeniodont locality (AMNH 125691) has a low (length)/(width) ratio, indicating that it probably represents *Phenacodus intermedius* and not *P. grangeri*. This suggests that the age of this locality is Clarkforkian. The level of the Second Taeniodont locality is stratigraphically between the "?late Tiffanian or Clarkforkian" and "middle Clarkforkian" levels of McKenna (1980:329). West and Atkins (1970) described a Bridgerian specimen of *Phenacodus intermedius* from the Tabernacle Butte area. This specimen (AMNH 56053) is an isolated unworn upper molar which lacks all dentine as well as its roots. It probably represents an unerupted tooth.

P. intermedius is also known from the Clarkforkian and *Heptodon* range zone of the Piceance Basin. A supposed Clarkforkian P⁴ from the Piceance Basin (FMNH.P 26874) has a (length)/(width) ratio of 0.89 and is intermediate in this respect between *P. grangeri* and *P. intermedius*. I consider it tentatively *P. intermedius*.

Referred specimens.—Powder River Basin, Wasatchian: AMNH 56192–56195 and UCM 54750. Bighorn Basin, *Plesiadapis gingerichi* zone: UM 68404, 68405, 68408, 68416, 68422, 68424, 68431, 68727, 68729, 68735, 68736, 68750, 68753, 68754, 68886, 68887, 68889, 71297, 71301, 71612, 71619, 71797, 71798, 71800, 71805, 71807, 71822, 73330, 73336, 73338, 73340, 73361, 73721, 73724, 85249, 85251, 88228, YPM-PU 18123, 18937, 18974, 20167, and 20313; *Plesiadapis cookei* zone: UM 63278, 65003, 65004, 65036, 65239, 65258, 65476, 65480, 65482, 65487, 65490, 65495, 65522, 65527, 65542, 65546, 65642, 65663, 65721, 66211, 66322, 66327, 66336, 66497, 66507, 66508, 66537, 66627, 66635, 66636, 66643, 66719, 66753, 66758, 66761, 66923, 67019, 67022, 67026, 67029, 67030, 67201, 67221, 67354, 67357, 67359, 68228, 68231, 68293, 68517, 68881, 69223, 69261, 69266, 69299, 69337, 69340, 69672, 69677, 69678, 69912, 71176, 71179, 71186, 71237, 71441, 71448, 71457, 71463, 71466–71469, 71473, 71474, 71632, 76870, 77349, 80244, 80254, 80260, 80269, 80336, 80340, 80343, 80567, 82006, 82015, 82248, 82365, 82391, 82506, 82621, 83194, 83757, 83759, 83808, 86146, 86156, 86157, 86250, 86260, 86263, 86559, 86560, 87799, 87810, 87824, 87830, 87995, 87999, 88173, 93237, YPM-PU 13206, 18083,

18142, 18170, 19452, 19453, 19521, 20097, 20108, 20114, 20115, 20119, 20167, 20169–20171, 20260, and 20265; *Phenacodus-Ectocion* zone: UM 64711, 64716, 65063, 65079–65081, 66155, 66169, 66186, 66294, 66295, 66300, 66313, 66317–66319, 66550, 66552, 66553, 66578, 66582, 66586, 66593–66595, 67243, 68037, 68041, 68042, 68208, 68222, 68223, 69359, 69866, 69876, 69880, 69883, 69886, 69890, 71354, 71423, 71480, 73603, 73726, 80438, 81913, 83198, 83199, 83428, 83436, 83619, 83785, 83799, 83800, 83803, 88158, 91464, YPM-PU 18045, 18148, 18174, 20096, 20107, 20110, 20116, 20121–20123, and 20126; *Cantius torresi* zone: UM 63570; Lower *Haplomylus-Ectocion* zone: UM 63951, 64597, 64678, 65339, 65500, 66250, 66253, 66410, 66510, 66517, 66526, 66900, 67117, 67257, 68470, 68524, 69407, 69558, 69581, 71259, 72137, 75928, 76377, 76384, 76488, 76679, 77111, 77112, 77205, 77223, 77227, 79610, 79813, 80189, 80305, 80398, 82644, 82707, 82796, 83130, 83309, 83337, 83349, 83511, 83777, 84745, 85934, 85941, 85963, 85977, 86740, 86764, 86846, 86892, 86976, 87047, 87137, 87148, 87198, 87314, 87327, 87332, 87368, 87500, 87562, 87746, 87769, 87928, 88027, 91004, 92115, 92124, USGS 1808, 1909, 1910, 2312–2315, 2420, 2497, 3569, 4313, 4392, 5037, 7116, 8164, 8246, 8247, 8798, 8939, 9057, 9321, 19300–19302, UW 6280, 7453, 7454, 7458, 7460, 7463, 7464, 7466, 7469, 7471–7475, 7477–7481, 9272–9274, 9276, 9280, 9283, 10000, 10130, 10331, 10343, YPM 22977, 22985, 22986, 23001, 23019, 23022, 26787, 26985, 31946, 31970, 31990, 32033, 32189, 32201, 32228, 32415, 32433, 32523, 32778, 32792, 34301, 34302, 34971, 35980, 35984, 35989–35991, 35994, 35996, 36011, 36018, 35019, 36673, 36675, 37832, 37833, 37838, 37839, 37849, YPM-PU 18154, 20117, and 23232; Upper *Haplomylus-Ectocion* zone: UM 66697, 66836, 67046, 69156, 69947, 71196, 71197, 71542, 73017, 73806, 73937, 76815, 78950, 78984, 79200, 79226, 79288, 81867, 82863, 82955, 82995, 83526, 85719, 87612, 88089, USGS 4390, 7083, YPM 23002, 26566, 26581, 31944, 32203, 35959, YPM-PU 17883, 18154, 20109, and 20113; *Bunophorus* zone: UM 64139, 82588, USGS 7918, 10204, and YPM 32057; *Heptodon* zone: USGS 701, 967, 5761, YPM 18633, 22998, 36025, 36684, and 37836; *Lambdotherium* zone: YPM 36685; Clarkforkian: AMNH 22197, UM 77287, 85394, 85417, 85421, 86803, 87204, YPM-PU 17713, 19523, 19593, 20097, 20112, and 20268; Wasatchian: AMNH 4369, 15777, UM 63586, 63600, 63601, 63603, 63609, 63629, 63657, 63664, 63665, 63696, 63699, 63702, 63703, 63707, 63713, 63761, 63768, 63809, 63888, 63898, 63903, 63914, 63936, 82649, 85254, 87069, 87175, 87218, 87229, 87232, 87239, YPM 25904, 25924, 27227, and YPM-PU 20098. Meeteetse area, Wasatchian: UW 14552. North Fork of Shoshone River, *Lambdotherium* zone: UM 80847 and YPM-PU 18041. Wind River Basin, *Plesiadapis cookei* zone: AMNH 56129, 56133, 56134, 57221, 57281, 57283, 57292, 57297, 86835, 86894, and 125693; *Lambdotherium* zone: AMNH 14784, 14790–14796, CM 12476, 22349, 22352, 22353, 43190, 43676, MCZ 3492, UCM 45646, 46424, 46641, and YPM-PU 20146; *Palaeosyops* zone: CM 22344, 36458, 37326, and 43674; Clarkforkian: AMNH 86856, 86915, 88127, and 125691; Wasatchian: AMNH 4822 and UW 17335. Green River Basin, Clarkforkian: CM 8813, USNM 20644, 20649, 21287, 409470, 409472–409474, 409476, and USNM field number 29–61 (in part); *Lambdotherium* zone: FMNH.PM 15507; Bridgerian: AMNH 56053. Washakie Basin, *Plesiadapis cookei* zone: UCMP 13391–13394, 133936, 133939, and 133941–133944; Lower *Haplomylus-Ectocion* zone: UCM 28949, 29139, UCMP 44050, 44791, 46188, 46190, 46191, and 58283. Laramie Basin, Wasatchian: UW 1, 3, 10038, 10040, 10041, and 10507. Piceance Basin, Clarkforkian: DMNH 2152, FMNH.PM 208, 212, 218, 529, P 14938, 15005–15007, 15521, 15522, 15525, 15537, 15539, 15567, 15645, 15708, 26064, 26065, 26070, 26081, 26092, 26093, 26099, 26130, 26688, 26874, 27146, 27384, and UCM 48642; Wasatchian: FMNH.PM 331, P 15690, 26454, 26573, 26887, and UCM 40731. Huerfano Basin, *Lambdotherium* zone: UCM 38258. Big Bend National Park, Wasatchian: TMM-TAMU 40143–1. San Juan Basin, *Heptodon* zone: AMNH 16246, 55488, 80730 (in part), CM 46868, and 46869.
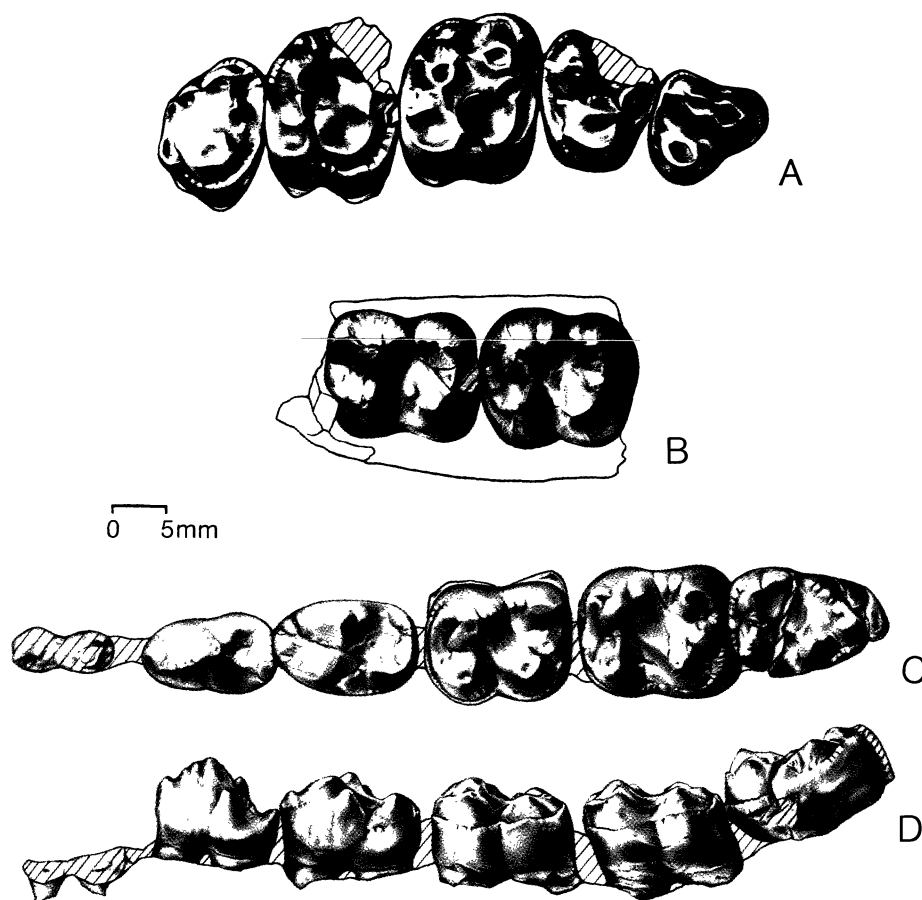
Figure 40. Dentition of *Phenacodus trilobatus*. A, P³-M³ (AMNH 14786), *Lambdotherium* zone of Wind River Basin, occlusal view. B, M₁₋₂ (UM 77446), Lower *Haplomylus-Ectocion* zone of the Clarks Fork Basin, occlusal view. C and D, P₃-M₃ (AMNH 15275), holotype of junior synonym *Phenacodus robustus* from the Wasatchian of the Bighorn Basin, occlusal and labial view.

Phenacodus trilobatus Cope, 1882
Figure 40

P. trilobatus Cope, 1882f, p. 179; Cope, 1885, p. 463, pl. 25e:16.88

P. primaevus robustus Granger, 1915, p. 340, fig. 3, 5, and 7.

P. primaevus primaevus, Kelley and Wood, 1954, p. 349, fig. 7b.

P. primaevus (in part), McKenna, 1960, p. 99; Guthrie, 1967, p. 38; Guthrie, 1971, p. 81; West, 1976, p. 33; Bown, 1979, p. 97; Davidson, 1987, p. 114.

P. robustus, Guthrie, 1971, p. 81.

Holotype.—AMNH 4679, left dentary with M₁₋₃, collected at an unknown locality in the Bighorn Basin by J. L. Wortman in 1880.

Range and distribution.—Lower *Haplomylus-Ectocion* through *Lambdotherium* zone of the Wasatchian from the Williston, Powder River, Bighorn, Wind River, Washakie, Laramie, Piceance, and San Juan Basins.

Diagnosis.—Comparable in size to *P. magnus,* larger than all other phenacodontids. P₄ trigonid basin wide, molar trigonid basin long, unlike *P. magnus.* P⁴ is approxi-

mately as long as it is wide, and has a small parastyle unlike *P. magnus.*

Description.—All teeth except I₁ are present in a crushed skull of *Phenacodus trilobatus* from the McCullough Peaks in the Bighorn Basin (YPM-PU 14717). The dentition of this individual is worn, but resembles that of *Phenacodus intermedius* in most non-diagnostic features.

P. trilobatus and *P. magnus* are similar in size, and are best distinguished on the basis of the width of the trigonid basin of P₄, the shape of the trigonid of the lower molars (see description of *P. magnus*), and the outline shape of P⁴ (Table 5). As discussed before, principal component analysis distinguishes well between *Phenacodus intermedius* and *Phenacodus trilobatus.* Specimens in which one or more of the measures used in the principal component analysis cannot be measured are sometimes not identifiable.

Discussion.—Granger (1915) distinguished three subspe-

cies of *P. primaevus*. Granger's (1915) subspecies are: *P. p. hemiconus*, *P. p. robustus* and (not stated explicitly, but rater implied) *P. p. primaevus*. He diagnosed *P. primaevus robustus* from *P. primaevus primaevus* by its wider cheek teeth and more robust limb bones. The presently available large sample indicates that the (length)/(width) ratio of the teeth does not separate two morphs within *Phenacodus trilobatus*. Granger (1915) gave subspecific status to Cope's (1882a) *P. hemiconus*, and distinguished it from other subspecies on the basis of size and shape details of M^3. These characters appear not to be bimodal in the present sample, and I therefore follow most authors in disregarding Granger's subspecies. The oldest unambiguous name for this taxon is *Phenacodus trilobatus*, older names are based on ambiguous holotypes (see discussion of genus).

Guthrie (1971) and Schankler (1981) recognized the distinctness of *Phenacodus trilobatus* from *Phenacodus intermedius*, but used different names for the two taxa. Guthrie (1971) synonymized the smaller predominantly early Wasatchian *Phenacodus intermedius* with *P. primaevus* Cope, 1873, and retained *Phenacodus robustus* for larger specimens here called *P. trilobatus*. Schankler (1981) followed Granger (1915), and referred larger *Phenacodus* to *P. primaevus*, and smaller forms to *P. intermedius*. Granger's (1915) concept of *P. primaevus* was mainly based on a skull and skeleton that he chose to be the plesiotype for *P. primaevus* (AMNH 4369), but, as pointed out before, the holotype of *P. primaevus* is a nondiagnostic M$_3$.

P. trilobatus is known from an undescribed locality in the Bearpaw Mountains of Montana (USNM accession number SVH69–18A), and from two specimens in the early Wasatchian of the Powder River Basin (USNM locality indication "Sussex-22–51"). Delson (1971) did not discuss these specimens.

Phenacodus trilobatus appears in the early Wasatchian of the Bighorn Basin at 1665 m in the Clarks Fork Basin section. The highest occurrence of *P. trilobatus* in the central Bighorn Basin is at 625 m (*Heptodon* zone). *Phenacodus trilobatus* is not known from the *Lambdotherium* zone of the Bighorn Basin. The Indian Meadows Formation of the Wind River Basin has yielded several specimens of *P. trilobatus* from locality 13E of Keefer (1965; unnumbered specimens in the USNM collection), and from localities near the Boysen Reservoir (UW 17333, 17334, and 17336).

Referred specimens.—Powder River Basin, Wasatchian: USNM accession number Sussex 22–51. Bearpaw Mountains, Wasatchian: USNM accession number SVH 69–18 (in part). Bighorn Basin, Lower *Haplomylus-Ectocion* zone: UM 69596, 77446, 82708, 87896, USGS 19216, UW 7470, 9277, YPM 23015, 25222, and 36694; Upper *Haplomylus-Ectocion* zone: UM 65757, 67272, 67295, 67342, 71512, 73000, 73018, 73031, 73556, 75736, 76438, 79440, 79459, 80726, 83683, 85654, 86823, 86826, 86996, 87009, 87622, USGS 702, 1770, 1785, 2223, 2246, 3668, 4312, 4315, 4319–4321, 4340–4345, 4348–4350, 4354–4357, 4359–4361, 4363–4366, 4369, 4374, 4375, 4389, 4391, 4393–4401, 4407–

4416, 4424–4426, 6074, 7006, 7024, 7025, 7258, 7356, 7937, 7942, 7951, 8010, 8335, 8369, 8727, 8923, 8974, 9000, 9001, 9726, 9759, 10165, 10178, 10181, 10215, 10217, 10456, 13716, 17883, 17884, 18288, 18294, 18319, 18320, 18321, 19288–19290, 19311, 19317, 19320, YPM 13328, 13329, 23009, 23016, 23018, 25193, 25254, 25288, 25298, 25311, 25326, 25482, 25494, 25745, 25748, 25918, 26091, 26456, 27185, 27191, 27228, 27490, 28456, 31939, 32073, 32085, 32192, 32402, 32952, 32959, 34299, 35955, 35960, 35972, 35979, 35998, 36000, 36015, 36022, 36031, 36664, 36687, 36692, 36704, 37842, 37844, 37854–37857, 38041, and 41421; *Bunophorus* zone: UM 64073, 64078, 64127, 64157, 64498, 86941, 86957, 87126, USGS 3560, 4310, 4402, 7245, 7248, 7552–7554, 7758, 7759, 8589, 8864, 10173, 10194, 10203, 17872, 17878, 17879, 19280, 19294, 19295, YPM 17690–17692, 17698, 18597, 25313, 26687, 32003, 32526, 32632, 32755, and 35952; *Heptodon* zone: USGS 1874, 2207, 2225, 6289, 8922, and YPM 23401; Wasatchian: AMNH 15275, UM 64311, 77060, 90964, 92220, USGS 2207, 4311, 7042, 7082, 8229, 8386, 8901, 9135, 17882, 18324, 19269, 23011, 23013, 23017, 23023, 32132, 32694, 36662, YPM 25732, 25900, 33106, YPM-PU 14717, and 16162. Wind River Basin, *Heptodon* zone: ACM 3025; *Lambdotherium* zone: AMNH 14786; Wasatchian: UW 17333, 17334, and 17336. Washakie Basin, Lower *Haplomylus-Ectocion* zone: UCMP 43958, 44796, 46189, 117306, 117308, and 117310–117315,. Laramie Basin, Wasatchian: UW 6960 and 76019. Piceance Basin, Wasatchian: FMNH.PM 271, 275, 281, P 14970, 15622, 15652, 15668, 15681, 15697, 26449, 26458, 26465, 26515, 76019, UCM 40732, 40734, 41175, 41265, and 41273. San Juan Basin, *Heptodon* zone: AMNH 16247, 80702, 80711, 80730, 113158, USNM 1004, 1019, 1026, and 5381.

Phenacodus teilhardi Simpson, 1929
Fig. 41

Phenacodus europaeus Teilhard de Chardin, 1927, p. 21, pl. 5:16–18.
Phenacodus teilhardi Simpson, 1929b, p. 13; Rich, 1971, p. 45.

Holotype.—No type specimen was designated for *Phenacodus teilhardi* until Rich (1971) chose an unworn right upper molar from Dormaal as such (IRSNB M88). The specimen was figured by Teilhard de Chardin (1927, pl. 5:16).

Range and distribution.—The locality Dormaal in the Paris Basin. Dormaalian (early Eocene).

Diagnosis.—Smaller than other European *Phenacodus*. Size similar to *Phenacodus vortmani*, but enamel more crenulated. P$_3$ short, unlike *P. vortmani*.

Description.—Only isolated teeth and a metapodial (IRSNB M91) are known for *Phenacodus teilhardi*. Known teeth include a single P$_3$, P^3, D^3, one lower molar, and four upper molars. The teeth of *P. teilhardi* are strongly crenulated and differ as such from *P. vortmani*. Crenulation is a variable character in phenacodontids as pointed out by Rich (1971), but in general large *Phenacodus* are more crenulated than small taxa. The strong crenulation of *P. teilhardi* is surprising when compared to *P. vortmani*, which is of approximately the same size. Crenulation can serve tentatively to distinguish these taxa. The only P$_3$ known for *P. teilhardi* is shorter than P$_3$ of *P. vortmani*, and more rounded anteriorly. This morphology agrees well the short jaw in the holotype of *P. lemoinei* and suggest that both these European *Phenacodus* had a short jaw.

Discussion.—*Phenacodus teilhardi* Simpson, 1929b, was originally described as *Phenacodus europaeus* Teil-
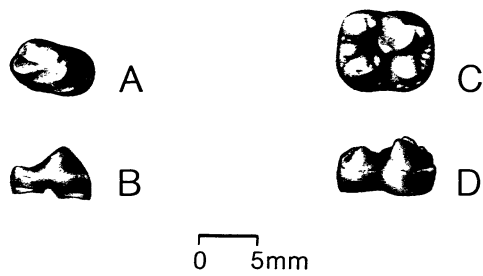
Figure 41. Dentition of *Phenacodus teilhardi* from Dormaal. A and B, P$_3$ (IRSNB A), occlusal and labial view. C and D, M$_1$ or M$_2$ (IRSNB M90), occlusal and labial view.

Figure 42. Dentition of *Phenacodus lemoinei*. A and B, M$_3$ (MNHN AL-803) from a locality near Epernay, occlusal and labial view.

hard de Chardin, 1927. The latter name is a homonym of *Phenacodus europaeus* Ruetimeyer, 1888, a taxon now referred to the artiodactyl *Meniscodon* (Teilhard de Chardin, 1927; Simpson, 1929c).

P. teilhardi is not known from the locality Pourcy although Pourcy and Dormaal are similar in age (D. E. Russell, 1982; D. E. Russell et al., 1982; Godinot, 1988). Only two poorly preserved specimens of *Phenacodus* are known from Pourcy. Py-59-L is a highly abraded lower molar, and MNHN PY-16144 is an isolated trigonid. These two specimens are larger than *P. teilhardi*, and I identify these tentatively as *P. lemoinei*. If Dormaal and Pourcy yield contemporaneous faunas, than two *Phenacodus* lineages coexisted in the Dormaalian of Europe.

Referred material.—Dormaal, Dormaalian: Do-11-Bn, Do-1911-Wo, IRSNB Do-65, M88, M89, M90, M91, A, and B.

Phenacodus lemoinei, new species
Fig. 42

Plesiesthonyx munieri (in part) Lemoine, 1891, p. 276, fig. 31.
Phenacodus sp., Teilhard de Chardin, 1922, p. 64, fig. 31, pl. 3:15–16.
Phenacodus cf. *P. teilhardi*, Rich, 1971, p. 45, fig. 14. West, 1971, p. 22, fig. 8c.

Holotype.—Mu-250-L, dentary with P$_4$-M$_3$, and alveoli for right P$_3$, and left and right I$_1$, C$_1$, P$_{1-2}$. The specimen was described and figured by Rich (1971) and recovered at Mutigny in the Paris Basin. Its age is Dormaalian.

Range and distribution.—Dormaalian and Grauvesian (early Eocene) of the Paris Basin.

Diagnosis.—Intermediate in size between *P. teilhardi* and *P. condali*, similar in size to Wasatchian *P. intermedius*. Lower jaw short and mandibular symphysis fused, unlike North American *Phenacodus*. Lower molars wide, and M^3 with strong lingual cingulum, unlike *P. intermedius*.

Description.—In addition to the holotype, only isolated cheek teeth are known for *P. lemoinei*. They include three M$_1$ or M$_2$s, two M$_3$s, a P^4, a D^4, and two M^{3}s. Direct comparison of contemporaneous *P. teilhardi* and *P. lemoinei* is only possible for lower anterior molars. *P.*
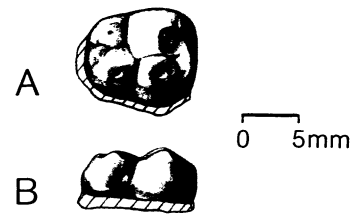
lemoinei differs from *P. teilhardi* by the inflated cusps of the lower molars and by its larger size. *P. lemoinei* has a short dentary with no diastemata between any teeth from C$_1$ to P$_4$, a fused symphysis and wide anterior lower molars (Table 7). In these characters *P. lemoinei* differs from all North American *Phenacodus*. The two known M^{3}s of *P. lemoinei* (MNHN AL-5176 and 5177) have a complete lingual cingulum. This character occurs infrequently in North American *Phenacodus*, and can be used tentatively to diagnose *P. lemoinei*.

Table 7. W/L ratios for North American and European *Phenacodus* (data on *P. condali* from Crusafont and Villalta, 1954).

	N	Mean	SD	Max
North America				
P. vortmani				
P$_4$	153	0.67	0.05	0.68
M$_1$	163	0.84	0.05	0.98
M$_2$	176	0.87	0.05	0.98
P. intermedius				
P$_4$	38	0.68	0.04	0.75
M$_1$	35	0.83	0.04	0.91
M$_2$	47	0.90	0.04	0.96
Europe				
P. teilhardi				
M$_1$ or M$_2$	1	0.80		
P. lemoinei				
M$_1$	1	0.99		
M$_2$	1	1.04		
P. condali				
P$_4$	1	0.73		
M$_1$	1	0.89		
M$_2$	1	1.00		

Discussion.—Rich (1971) described a M$_3$ of *Phenacodus lemoinei* from Mutigny and cited UCMP 65553 as its specimen number. UCMP 65553 is the number of a cast of the M$_3$ in the UCMP collections, the number of the original is MNHN AL-5550. An M$_3$ from "Epernay"

(MNHN AL-803) has been mislabelled as *Tricuspiodon* from the Paleocene locality Cernay (D. E. Russell, 1980).

P. lemoinei and *P. teilhardi* are both known from the earliest Eocene Dormaalian, although they do not co-occur at any locality. *P. lemoinei* is also known from later Eocene localities.

Etymology.—Lemoinei, named for Dr. Victor Lemoine, who was the first to describe and figure teeth of *P. lemoinei.*

Referred material.—Mutigny, Dormaalian: MNHN AL-5550, Mu-196-L, and Mu-250-L. Pourcy, Dormaalian: MNHN Py-16144 and Py-59-L. Grauves, Grauvesian: MNHN Gr-83-L. One or more unknown localities near Epernay: MNHN AL-803 and AL-5176–5178.

Phenacodus condali (Crusafont and Villalta, 1955)

Almogaver condali Crusafont and Villalta, 1955, p. 9, pl. 13–14.

Holotype and only known specimen.—Right dentary with alveoli for P_2, P_3 fragments, and P_4-M_3. The specimen was found "high in the Eocene Formation" of the Sierra de Montllobar, southwest of Tremp (Crusafont and Villalta, 1955). Tremp is in the Tremp Basin in northeastern Spain.

Range and distribution.—Robiacian (middle Eocene) of the Sierra de Montllobar in the Tremp Basin.

Diagnosis.—Larger than other European *Phenacodus,* comparable to Wasatchian *Phenacodus trilobatus.* Dentary short, unlike *P. trilobatus.* P_4, M_1, and M_2 wider than *P. trilobatus.*

Description.—I have not seen the original or a cast of the type and only specimen of *Phenacodus condali,* and base my comparisons on the description and figures of Crusafont and Villaltae (1955). *P. condali* differs from *Phenacodus lemoinei* by its larger size, and by the wider P_4. It agrees with *P. lemoinei* in the absence of diastemata between P_{2-4}, the short dentary, and the wide M_2 (Table 7).

P. lemoinei and *P. condali* differ from North American *Phenacodus* in having wider molars and a shorter jaw. Rich (1971) cited many morphological differences between the holotypes of *P. condali* and *P. intermedius,* but most of these fall within the normal range of variation of *Phenacodus* known from larger samples.

Copecion Gingerich, 1989

Phenacodus (in part), Cope, 1885, p. 428; Granger, 1915, p. 332; West, 1976, p. 19.
Copecion Gingerich, 1989, p. 52.

Type of genus.—C. davisi Gingerich, 1989.
Referred taxon.—C. brachypternus (Cope, 1882a).
Age and Distribution.—Clarkforkian and Wasatchian land-mammal ages of western North America.

Diagnosis.—Differs from all other phenacodontids in the elongate P_3 and P_4, with long trigonid basin, and elongate P^3 and P^4. Differs from *Ectocion* by being more bunodont. P_3 without metaconid and with weak hypoconid, unlike *Ectocion.* Paracristid usually ends high on the lingual side of the molars and paraconid absent, unlike *Ectocion.*

Parastyle and mesostyle of upper molars weak, unlike *Ectocion.* M^3 hypocone weak or absent, unlike *Phenacodus.* Mesostyle present, unlike *Tetraclaenodon.*

Description.—Copecion is characterized by an elongate P_2, P_3, P_4, P^3, and P^4. Elongation is most pronounced in the trigonid of the lower premolars. *Copecion* resembles *Phenacodus* in other known dental characters, it is bunodont, its paracristid ascends the metaconid, and the mesostyle is large but smaller than in *Ectocion.* The mandibular symphysis is usually unfused. Judging from postcranial elements, *Copecion* is more cursorial than *Phenacodus* (Chapter VI).

Discussion.—Cope (1882a) referred the initial sample of *Copecion brachypternus* to *Phenacodus.* He was followed in this by subsequent authors until Gingerich (1989) proposed *Copecion* for *C. brachypternus* and *C. davisi.* *Copecion* is morphologically closer to *Phenacodus* than to *Ectocion.* It is bunodont, has a small hypoconid on P_3 and weak mesostyle and parastyle on the upper molars. In size *Copecion* is easily confused with *Ectocion.*

Copecion brachypternus (Cope, 1882)
Fig. 43

Phenacodus brachypternus Cope, 1882a, p. 180; Cope, 1885, p. 490, fig. 25e:14; Granger, 1915, p. 344, fig. 4b, 6b, 8b, and 10; Guthrie, 1967, p. 38; Delson, 1971, p. 345; West, 1971, p. 14, fig. 10; Bown, 1979, p. 99, fig. 55d; Davidson, 1987, p. 115.
Phenacodus? *brachypternus,* McKenna, 1960, p. 99, fig. 53.
?Phenacodus sp., McKenna, 1960, p. 101, fig. 54.
Phenacodus, cf. *brachypternus,* Gazin, 1962, p. 66.
Ectocion osbornianus (in part), Rose, 1981, p. 73.

Holotype.—Cope did not designate a holotype in his initial descriptions of the *C. brachypternus* (1882a, 1885), but referred three mandibles from the Bighorn Basin to the taxon. Granger (1915) designated one of these, AMNH 4396, as the holotype. It is a partial left dentary with P_3-M_3, found in "Gray Bull Beds, Bighorn Basin, Wyo. J. L. Wortman, 1881" (Granger, 1915:344).

Age and distribution.—Plesiadapis cookei zone of the Clarkforkian through *Heptodon* zone of the Wasatchian from the Powder River, Bighorn, Wind River, Green River, Great Divide, Washakie, Laramie, Piceance, and San Juan Basins.

Diagnosis.—Similar in size to *Ectocion osbornianus,* smaller than *Phenacodus vortmani,* larger than *Copecion davisi.* No shape differences are apparent between different *Copecion.*

Description.—All teeth except the upper incisors are known for *C. brachypternus,* West (1971) discussed the deciduous dentition, and a partial skeleton (UM 64179) is described in Chapter VI. Differences between *Ectocion osbornianus* and *Copecion brachypternus* were discussed above. The mandibular symphysis of *C. brachypternus* is sometimes fused (UM 75285), but usually unfused (e. g., UM 64177).

Phenacodus vortmani is larger than *Copecion*
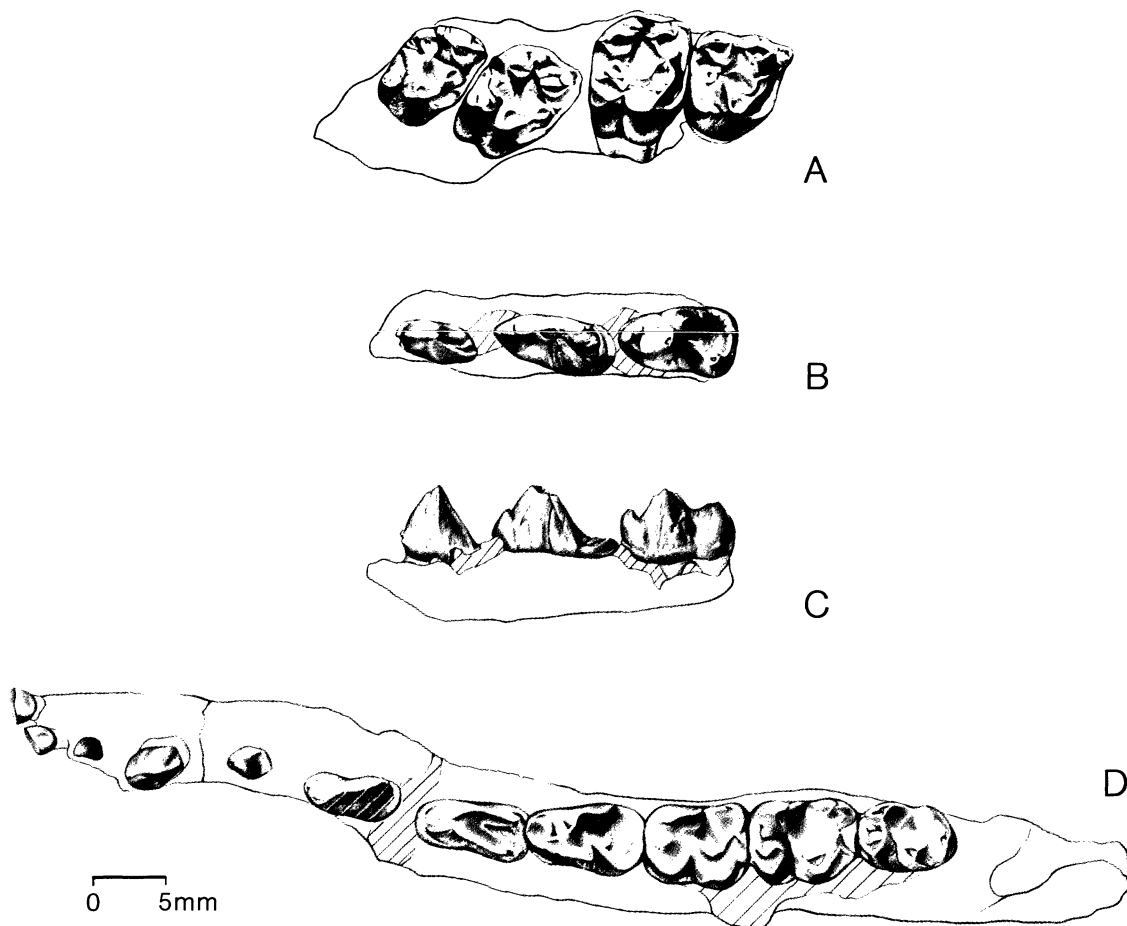
Figure 43. Dentition of *Copecion brachypternus* from the Wasatchian of the Bighorn Basin. A, P^4-M^3 (UM 64063) in occlusal view. B-C, P_{2-4} (USGS 19324) in occlusal and labial view. D, I_1, I_3-M_3 (UM 64179) in occlusal view.

brachypternus and has a short P_3, P_4, and P^3, and a wide trigonid basin on P_4 (Table 6). Cusps of the upper molars of *P. vortmani* are more bunodont than in *Copecion*, and the hypocone of M^3 is usually stronger. The entoconid of P_4 is absent in 94% of *Copecion brachypternus* (N=63), but in only 15% of *Phenacodus vortmani* (N=173).

Discussion.—No evolution is apparent in tooth size in *Copecion brachypternus* (Figs. 44 to 48), but the taxon is not static. Evolution in shape is apparent in the scores on PC-2 in a principal component analysis of length and width of M_1 and M_2 (Fig. 48). These scores are closer to zero in the *Bunophorus* and *Heptodon* zones than in the Lower *Haplomylus-Ectocion* zone. PC-2 scores express mainly variability in width of M_1 and M_2 and length of M_2. The width dimensions load positively and length of M_2 loads negatively on PC-2 (Table 8). This indicates that middle and late Wasatchian *Copecion brachypternus* has wider lower molars and shorter M_2s than early Wasatchian speci-

mens. These differences are subtle, there is a broad zone of overlap between the distributions of scores. Another change in the lineage of *C. brachypternus* is the decrease in mean length of M_3: in the *Bunophorus* zone it is 7.5 mm (N=9, SD=0.3), and in the *Heptodon* zone only 7.0 mm (N=28; SD=0.4). This difference is significant (p<.002).

C. brachypternus ranges between 1370 m (*Plesiadapis cookei* zone) in the Clarks Fork Basin section and 630 m (*Heptodon* zone) in the central Bighorn Basin section. Its stratigraphic range is not continuous, it has never been found in the Upper *Haplomylus-Ectocion* zone of the central Bighorn Basin. This led Schankler (1980, 1981) to propose that *C. brachypternus* might be locally extinct in that zone. The taxon is also absent in the Upper *Haplomylus-Ectocion* zone of the Clarks Fork Basin, but Badgley and Gingerich (1987) have shown that its absence could be an artifact of decreased sample size.
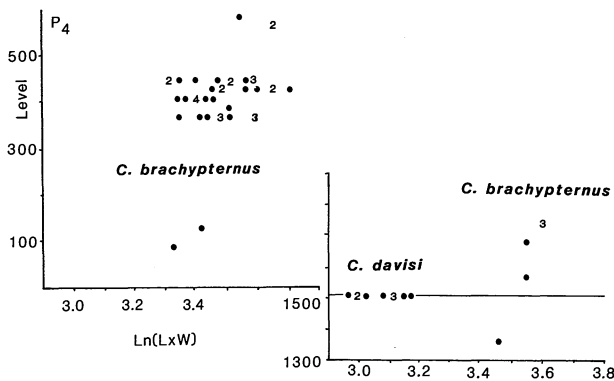
Figure 44. Scatter diagrams of natural logarithm of product of length and width (in mm) of P_4 for Bighorn Basin *Copecion davisi* and *C. brachypternus*. Ordinate is level in central Bighorn Basin section (left) and Clarks Fork Basin section (right). Horizontal line is boundary between Clarkforkian and Wasatchian.
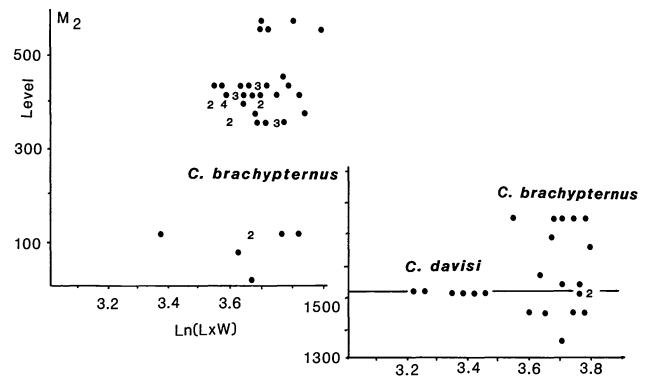
Figure 46. Scatter diagrams of natural logarithm of product of length and width (in mm) of M_2 for Bighorn Basin *Copecion davisi* and *C. brachypternus*. Ordinate is level (in meters) in central Bighorn Basin section (left) and Clarks Fork Basin section (right). Horizontal line is boundary between Clarkforkian and Wasatchian.
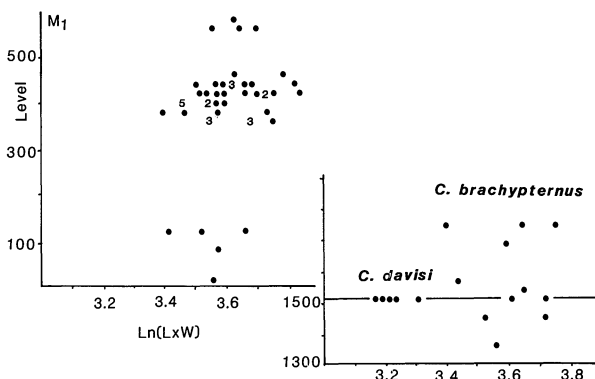
Figure 45. Scatter diagrams of natural logarithm of product of length and width (in mm) of M_1 for Bighorn Basin *Copecion davisi* and *C. brachypternus*. Ordinate is level in central Bighorn Basin section (left) and Clarks Fork Basin section (right). Horizontal line is boundary between Clarkforkian and Wasatchian.
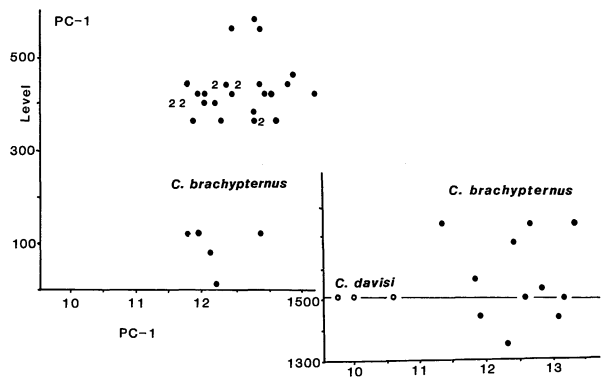
Figure 47. Scatter diagrams of principal component 1 of four lower molar measures for Bighorn Basin *Copecion davisi* and *C. brachypternus*. Dental measures analyzed are length and trigonid width of M_1 and M_2 (in mm). Ordinate is level (in meters) in central Bighorn Basin section (left) and Clarks Fork Basin section (right). Horizontal line is boundary between Clarkforkian and Wasatchian. Loadings are listed in Table 8.

Copecion brachypternus is rare in the Wind River Basin, where a single specimen is known from the *Heptodon* zone (AMNH 12788; Guthrie, 1967). Gazin (1962) reported an isolated phenacodontid molar from the locality Red Desert in the Great Divide Basin. I refer this specimen to *C. brachypternus* (USNM 205738).

McKenna (1960) described *Copecion brachypternus* from the Four Mile Fauna, and I also refer an isolated molar identified as ?*Phenacodus* sp. by McKenna to this taxon (UCMP 44048). McKenna's main criterion to not refer the specimen to *C. brachypternus* was apparently size, but these specimens are within the size range of the present sample of the taxon. Davidson (1987) described three specimens of *Copecion brachypternus* from the early

Wasatchian of the Laramie Basin. Judging from Davidson's measurements (1987:114), these specimens represent small individuals of *C. brachypternus*. *Copecion brachypternus* is also known from Clarkforkian through *Heptodon* range zone of the Wasatchian in the Piceance Basin.

Referred specimens.—Powder River Basin, Lower *Haplomylus-Ectocion* zone: AMNH 56187–56191, UCM 48627, and 52035. Bighorn Basin, *Plesiadapis cookei* zone: UM 88181; *Phenacodus-Ectocion* zone: UM 66297, 66852, 67234, 83195, 83648, 83793, 83795, 83802, and 92287; lower *Haplomylus-Ectocion* zone: UM 63814, 64839, 66352, 66607, 66870, 67137, 67141, 67434, 69450, 69806, 69813, 73868, 76417, 77014, 79626, 80069, 80684, 82643, 83128, 84715, 86746, 87520, 88164, USGS 8102, and 8326; *Bunophorus* zone: UM 64061, 64063, 64079, 64083, 64089, 64091, 64095, 64116, 64149, 64177,
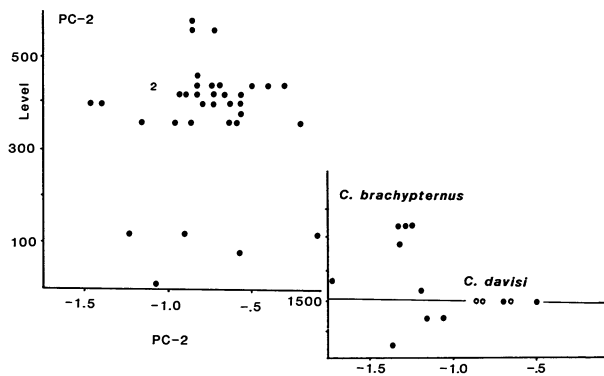
Figure 48. Scatter diagrams of principal component 2 of analysis of four lower molar measures for Bighorn Basin *Copecion davisi* and *C. brachypternus*. Dental measures analyzed are length and trigonid width of M_1 and M_2 (in mm). Ordinate is level (in meters) in central Bighorn Basin section (left) and Clarks Fork Basin section (right). Horizontal line is boundary between Clarkforkian and Wasatchian. Loadings are listed in Table 8.

Table 8. Principal component loadings of *Copecion* (N = 60).

Measure	PC-1	PC-2
% of variance	78.4	11.1
M_1, Length	0.59	–0.29
M_1, Width of trigonid	0.51	0.51
M_2, Length	0.45	–0.66
M_2, Width of trigonid	0.44	0.47

64179, 64181, 64289, 88342, USGS 1345, 3559, 4339, 7021, 7315, 7555–7561, 7628–7630, 9048, 9791, 9869, 10169, 10171, 10176, 10186, 10190–10193, 10195, 10198, 10201, 10204–10207, 10209, 10212, 17853, 17859, 17861, 17885, 18291–18293, 18299, 19301, 19298, 19318, 19319, 19321–19332, YPM 22964, 22973, 26333, 26401, 26500, 26634, 26671, 26694, 26875, 37860, 37864, 37867, 38086, 39526, and 41422; *Heptodon* zone: UM 64232, 83860, USGS 1201, 3692, 5111, 7150, 7557, 7558, 8487, 8534, 8705, 8770, 8895, 10167, 10195, 10196, 10206, 10481, 17863, 19219, 19306, UW 7465, 10008, 10490, YPM 17156, 17595, 17676, 17681, 17683, 21589, 22962, 23700, 26388, 26627, 27059, 29599, 32178, 32253, 32668, 32794, 34968, 34970, 36377, 36671, 36698, 36700, 36701, 37220, 37862, 37863, and 37865; Wasatchian: AMNH 15750, UM 63610, 63957, 75285, 75535, 75560,

85336, USGS 4386, 5282, 5286, 8184, 17868, 18325, 18329, YPM 18712, 25126, 28447, 32484, and 36666. Wind River Basin, *Heptodon* zone: AMNH 12788. Great Divide Basin, Wasatchian: USNM 205738. Washakie Basin, Lower *Haplomylus-Ectocion* zone: AMNH 80503, UCMP 44048, 44868, 46169, 46171, 46172, 46251, and 117303. Laramie Basin, Wasatchian: UW 10023, 10032, and 10034. Piceance Basin, Clarkforkian: FMNH.PM 223, P 16125 and 26107; Wasatchian: FMNH.PM 283, P 26654, 26719, 26838, UCM 40950, 41099, 41124, and 41184. San Juan Basin, *Heptodon* zone: AMNH 16249, 16250, 16253, 80701, 80704, 117162, CM 49466, 49467, 49469, 49471–49473, and USNM 214620.

Copecion davisi Gingerich, 1989
Fig. 49

Copecion davisi Gingerich, 1989, p. 53, fig. 35.

Holotype.—UM 86002, partial right dentary with P_3-M_3, and roots of C_1-P_2, from UM locality SC-67 at the south end of Polecat Bench in the Bighorn Basin (Gingerich, 1989). *Cantius torresi* zone.

Age and distribution.—*Cantius torresi* zone of the Wasatchian of the Powder River and Bighorn Basins.

Diagnosis.—Smaller than *C. brachypternus*, but similar in shape.

Description.—P_3 through M_3, and P^3 through M^3 are known for *C. davisi*. Gingerich (1989) described the hypodigm for the taxon. The shape of the teeth of *C. davisi* and *C. brachypternus* is similar, although the former is smaller (Figs. 44 to 48).

Copecion davisi co-exists with *Ectocion parvus* in the *Cantius torresi* zone, and the taxa are easily confused. The differences were discussed in the section on *E. parvus*.

Discussion.—*Copecion davisi* of the Bighorn Basin is restricted to the *Cantius torresi* zone. An M_3 of *Copecion davisi* (UCM 52888) was the only fossil recovered at a locality in the Powder River Basin. It extends the geographic range of *Copecion davisi* and also suggests that the *Cantius torresi* zone can be recognized in the Powder River Basin.

Referred specimens.—Powder River Basin, *Cantius torresi* zone: UCM 52888. Bighorn Basin, *Cantius torresi* zone: UM 66611, 69933, 71769, 71770, 74074, 75420, 75421, 83472, 83614, 83618 (in part), 83624, 83633, 83634, 83636 (in part), 83639, 83644, 83663, 83664, 83781, 83816, 83818, 83823, 83870, 83872, 86003, 86133, 86230, 87350, 87354 (in part), 87594, 87853, and 92348.
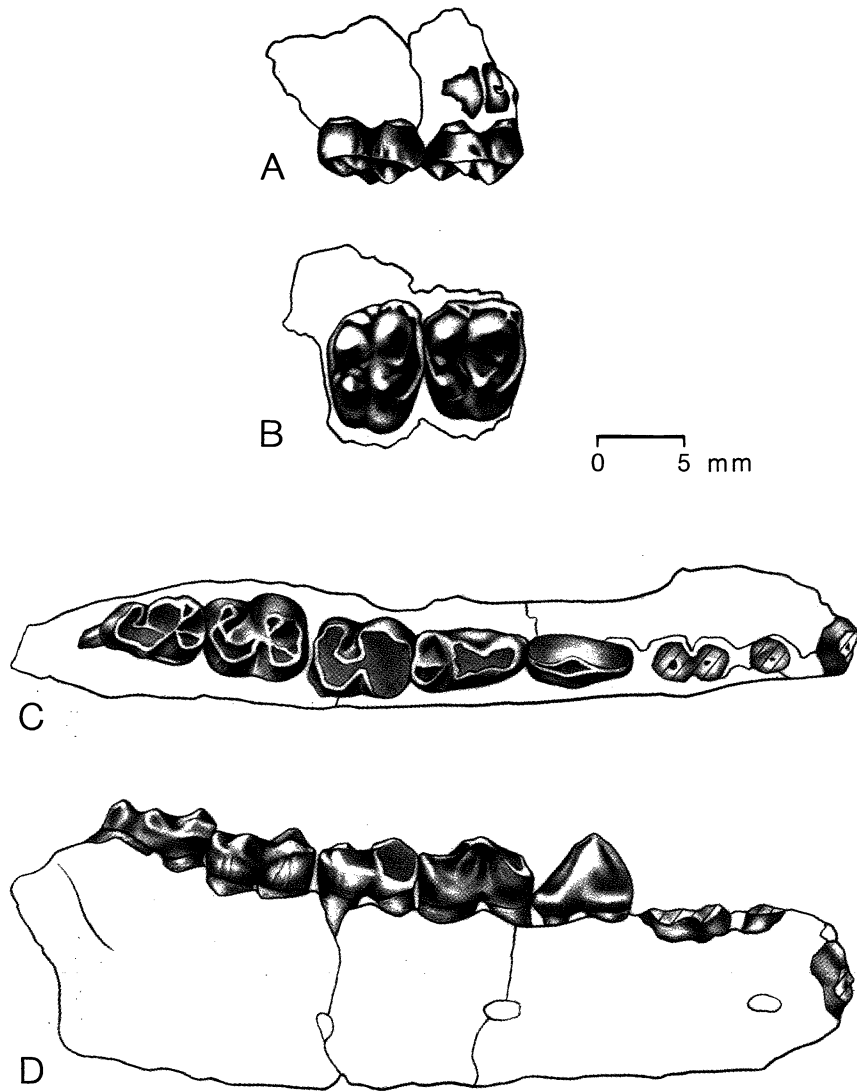
Figure 49. Dentition of *Copecion davisi* from Clarks Fork Basin. A and B, M^{1-2} (UM 83634), labial and occlusal view. C and D, P_3-M_3 (UM 86002), holotype in occlusal and labial view. Drawings reproduced from Gingerich (1989).

IV
THE PATTERN OF PHENACODONTID EVOLUTION

Phenacodontids are known from the middle Paleocene through early Eocene of North America and the early through middle Eocene of Europe. Here I will discuss the evolutionary pattern of phenacodontids chronologically by continent. I will also investigate some ecological factors that could have contributed to this pattern.

NORTH AMERICAN PHENACODONTIDAE

Torrejonian

The first phenacodontids are of the genus *Tetraclaenodon*, and they are known from the middle and late Torrejonian of the Western Interior. The most common taxon is *Tetraclaenodon puercensis*. It is abundant at Torrejonian localities ranging over nearly 20° of latitude, including northern faunas such as Rock Bench Quarry (N = 90) and southern faunas such as Big Pocket (N = 26). The wide range of the taxon across latitudes could be due to low climatic gradients during the Torrejonian (Upchurch and Wolfe, 1987).

The only other Torrejonian phenacodontid is *Tetraclaenodon septentrionalis*. This taxon is larger than *T. puercensis*, it is only known from a small part of the stratigraphic range of *T. puercensis*, and occurs only at a few localities in the northern part of the geographic range of the latter. The two taxa co-occur at a number of localities in the Crazy Mountains Basin.

Tiffanian

The boundary between Torrejonian and Tiffanian land-mammal ages is often characterized by the disappearance of *Tetraclaenodon* and the appearance of *Phenacodus* (Archibald et al., 1987). Both of these taxa are bunodont and identification of incomplete specimens as one or the other is sometimes problematical. The first representative of more lophodont *Ectocion*, *E. collinus*, also appears in the early Tiffanian. It is somewhat smaller than *T. puercensis*, whereas early Tiffanian *Phenacodus* is slightly smaller (*P. matthewi*) or similar in size (*P. bisonensis*) to *Tetraclaenodon*. Later *Ectocion* lineages may increase or decrease in size, whereas later North American *Phenacodus* are consistently larger than *P. matthewi*.

Tiffanian and Clarkforkian lineage segments of *Ectocion* display clear differences in premolar shape, especially in

P_3. The temporally consecutive lineages *E. collinus*, *E. mediotuber*, and *E. osbornianus* are characterized by increasing inflation of the protoconid and hypoconid on P_3. No intermediates between these three lineages have been found. There is no sufficiently fossiliferous stratigraphic section that straddles the boundary between *Plesiadapis rex* and *P. churchilli* zone faunas where intermediates between *E. collinus* and *E. mediotuber* are to be expected. Large samples of *E. mediotuber* and *E. osbornianus* are known from the Clarks Fork Basin section, but this section has not produced large numbers of fossils near the boundary zone of these taxa: no *Ectocion* specimens are known between 940 and 980 m level, a period of approximately 140,000 years (Gingerich, 1983).

A second *Ectocion* lineage, *E. cedrus*, appears in the middle Tiffanian. This taxon is known from quarry assemblages of the late Tiffanian, but it is not found at localities where contemporaneous *Ectocion mediotuber* occurs. The sedimentary environment of the quarries is different from that of localities in mudstones. Bartels (unpubl., 1987) interpreted the coarse-grained quarry assemblages of the Bighorn Basin as deposited in poorly-drained, near-channel sedimentary environments. It is possible that *E. cedrus* lived in poorly-drained environments, whereas contemporaneous *E. mediotuber* lived in the well-drained, more distal floodplain (Fig. 50). This interpretation is analogous to a similar distribution pattern in Tiffanian *Phenacodus* discussed below. Bighorn Basin *Ectocion cedrus* is not known from latest Tiffanian localities, which could be the result of real extinction or due to the absence of preserved assemblages from poorly-drained environments representing that time period.

No habitat specialization is apparent in early Tiffanian *Ectocion*. *E. collinus* is known from localities in mudstone deposits as well as in coarse-grained quarry assemblages. A specimen of *E. collinus* was found associated with *E. cedrus* at the middle Tiffanian locality Jepsen Quarry (unlabeled bar in "poorly-drained" row of Fig. 50). *E. collinus* may be ecologically more generalized than succeeding *Ectocion mediotuber*, which is exclusively found in well-drained sediments, and late Tiffanian *Ectocion cedrus*, which is only known from poorly-drained deposits.

Tiffanian *Ectocion* is mainly known from the northern half of the total geographic range of phenacodontids. Its most southern occurrence is in the Washakie Basin. It is not known from the Piceance Basin, although Clarkforkian

Pl. rex zone   **Pl. churchilli zone**   **Pl. simonsi zone**

Well drained

Pl. rex zone	Pl. churchilli zone	Pl. simonsi zone
127 E. cedrus	53	301
Ectocion collinus	E. mediotuber	E. mediotuber
Phenacodus bisonensis	P. grangeri	P. grangeri
P. grangeri	P. magnus	P. magnus

Poorly drained

Pl. rex zone	Pl. churchilli zone	Pl. simonsi zone
252 E. cedrus	79 E. cedrus	
P. grangeri	P. magnus	
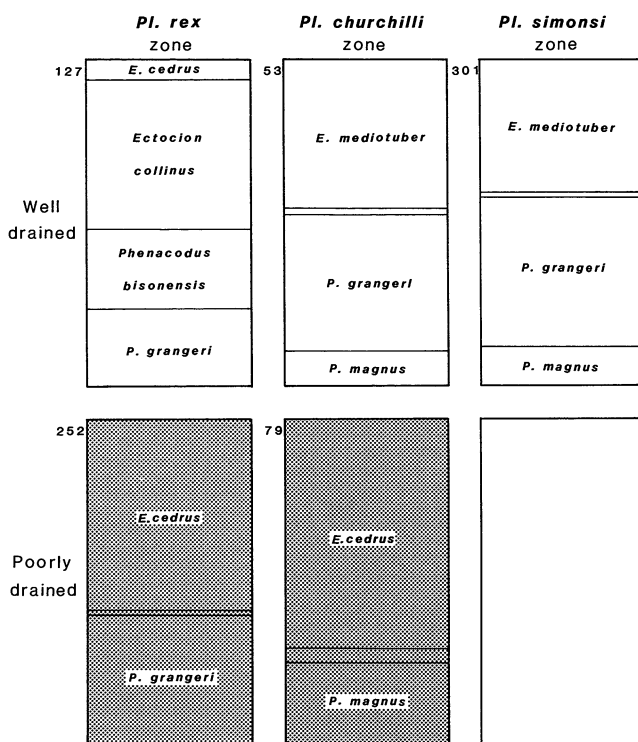
Figure 50. Habitat specialization of phenacodontids as reflected by their abundance in middle and late Tiffanian of Western North America. *Plesiadapis rex* zone of well-drained environments is dominated by *Ectocion collinus, Phenacodus bisonensis* and *P. grangeri*, whereas in poorly-drained environments *E. cedrus* and *P. grangeri* dominate (unlabeled bar is *E. collinus*). In late Tiffanian, well-drained environment is dominated by *Ectocion mediotuber* and *Phenacodus grangeri*, with weak representation of *P. vortmani* (unlabeled bars) and *P. magnus*. Poorly-drained environment of late Tiffanian is dominated by *E. cedrus* and *P. magnus*, with some representation of *P. grangeri* (unlabeled bar). Poorly-drained environment is not known from *Plesiadapis simonsi* zone. Numbers near left upper corner of bars represent numbers of specimens.

and Wasatchian localities in this basin have yielded *Ectocion*.

In contrast to *Ectocion*, morphological evolution in Tiffanian *Phenacodus* is slight. Minor morphological differences between lineages are apparent when large samples are studied, but variation within a population masks these differences in small samples. Two early Tiffanian *Phenacodus* lineages are known, *P. matthewi* and *P. bisonensis*. *Phenacodus matthewi* is rare, but ranged throughout the Tiffanian. It has only been recovered in the southern part of the range of phenacodontids. Near the northern border of its range it is even absent in such well sampled areas as the Bison Basin. The geographic and stratigraphic ranges of *Phenacodus matthewi* and of *Ectocion collinus* and *E. mediotuber* overlap in these areas, and *P. matthewi* has never been found with these *Ectocion* at one locality. These

taxa are similar in size, and the mutual exclusion could be the result of ecological similarity.

Phenacodus bisonensis is the second early Tiffanian *Phenacodus* lineage. It is similar in size to *Tetraclaenodon puercensis* and occurs throughout the Western Interior as does *Tetraclaenodon*. This is consistent with Hickey's (1980) observation that Torrejonian and Tiffanian floras from northern and southern areas have similar, low equitabilities: few taxa were abundant and many were rare. The distinction between early and middle Tiffanian *P. bisonensis* and late Tiffanian *P. vortmani* remains subtle at present. Early Tiffanian *P. bisonensis* is known from both mudstones (Gazin, 1956a) and quarry localities in sandstone (Krause and Gingerich, 1983). The taxon is absent at middle Tiffanian Cedar Point Quarry in spite of the enormous collections of other phenacodontids from this locality. Similarly, late Tiffanian *P. vortmani* is absent in quarry assemblages of the *Plesiadapis churchilli* zone of the Bighorn Basin, but common in floodplain deposits of the *P. simonsi* zone (Fig. 50). Distal floodplain deposits from the Bighorn Basin *P. churchilli* zone are poorly fossiliferous, but a specimen of *P. vortmani* has been recovered here (UM 71703, unlabeled bar in "well-drained" row of Fig. 50).

At least two explanations are possible for the occurrence of *Phenacodus vortmani* in the well-drained floodplain, but not in the poorly-drained environment of the late Tiffanian of the Bighorn Basin. *P. vortmani* could be locally rare in the Bighorn Basin in middle and early late Tiffanian. This is compatible with its absence in quarry samples, but inconsistent with the recovery of a specimen in the poorly fossiliferous distal floodplain deposits of the *Plesiadapis churchilli* zone. The pattern can also be explained by increasing habitat specialization of a lineage consisting of *P. bisonensis* and *P. vortmani*. In the early Tiffanian the lineage is found in both poorly-drained, near-channel environments (Douglass Quarry) and in well-drained, distal floodplain environments (Bison Basin). By the middle and late Tiffanian it is absent in poorly-drained sedimentary environments (Cedar Point and Love Quarries), but still present in well-drained floodplain deposits (mudstones of Bison and Bighorn Basins).

One lower molar of *Phenacodus grangeri* is reported from a presumed *Plesiadapis praecursor* zone locality in Big Bend National Park (Schiebout, 1974). With the exception of this specimen, the first record of *Phenacodus grangeri* is in the *Plesiadapis rex* zone. *P. magnus*, the largest Tiffanian phenacodontid, is found in deposits from the *Plesiadapis churchilli* and *P. rex* zones. *Phenacodus grangeri* and *P. magnus* are known from the entire latitudinal range of phenacodontids. Large fluctuations occur in the relative abundance of these taxa in the Bighorn Basin and these can be explained as differences in sedimentary environment similar to those in *P. vortmani* (Fig. 50). The distribution patterns of *P. magnus* and *P. grangeri* are apparently inversely correlated.

P. grangeri is abundant in the sample from Cedar Point Quarry in the *Plesiadapis rex* zone (N = 92). It is rare in the quarry assemblages from the *Plesiadapis churchilli* zone, where only a few specimens have been recovered (unlabeled bar in "poorly-drained" row of Fig. 50). It returns as the dominant *Phenacodus* in the floodplain deposits of the *Plesiadapis simonsi* zone. This distribution pattern is more or less reversed in *Phenacodus magnus,* which is absent in the *Plesiadapis rex* zone, and common in the *Plesiadapis churchilli* zone, but rare again in the *Plesiadapis simonsi* zone of the Clarks Fork Basin. Sedimentological differences between the coarse grained near-channel deposits and the fine grained floodplain deposits are consistent with proposed habitat differences in distribution of *Phenacodus grangeri* and *P. magnus. P. magnus* is dominant in the sedimentary environment of the *Plesiadapis churchilli* zone quarries, possibly indicating that it preferred poorly-drained habitat, while smaller *Phenacodus grangeri* mainly lived in the better drained sedimentary environment of the floodplain.

This does not explain the absence of *P. magnus* at Cedar Point Quarry from the *P. rex* zone. Cedar Point Quarry is sedimentologically more similar to the quarries from the *Plesiadapis churchilli* zone than to the floodplain deposits of the *P. rex* zone (Bartels, unpubl., 1987). At least two explanations are possible. One of these is that Cedar Point Quarry represents a low diversity fauna (Rose, 1981), lacking otherwise common taxa. Absence of *P. grangeri* would have been more likely than absence of *P. magnus* in this scenario, because habitat differences comparable to those of Cedar Point Quarry favored the latter in the *Plesiadapis churchilli* zone. Available evidence therefore supports the second hypothesis: introduction of *P. magnus* in the Bighorn Basin postdated the time of Cedar Point Quarry deposition and the habitat specialization of *P. grangeri.* In this scheme, the occurrence of *Phenacodus grangeri,* but not *P. magnus,* at Jepsen Quarry corroborates the age proposed for it by Gingerich (1976a): *Plesiadapis rex* zone.

The habitat specialization of late Tiffanian *Phenacodus* was apparently not as strict as that of late Tiffanian *Ectocion.* Late Tiffanian *Ectocion cedrus* is only known from coarse-grained quarry samples in which *E. mediotuber* is never found. One specimen of *Phenacodus grangeri* is known from late Tiffanian Croc Tooth Quarry. It co-occurs here with *P. magnus* and several specimens of the latter are also known from the floodplain deposits of the *P. simonsi* zone.

Summarizing, early Tiffanian *Ectocion collinus* and *Phenacodus bisonensis* of northern faunas are found in sediments representing several environments. In the late Tiffanian medium *Ectocion mediotuber,* medium *Phenacodus vortmani* and large *P. grangeri* are often found associated in well-drained environments. Late Tiffanian poorly-drained environments are characterized by small *Ectocion cedrus* and very large *Phenacodus magnus.* The distribution pattern of *Phenacodus* in the Tiffanian is reminiscent of that of Wasatchian phenacodontids in the Bighorn Basin. Schankler (1981) documented this pattern and suggested that ecological causes were the main factor in the distribution of these phenacodontids.

Clarkforkian and earliest Wasatchian

Phenacodontids are abundantly represented in Clarkforkian faunas of the Western Interior. More than 45% of Clarkforkian specimens from the Bighorn Basin are phenacodontids (Rose, 1981). Clarkforkian faunas are only known from the northern part of the total range of phenacodontids and it is therefore not clear if phenacodontids in them were geographically restricted. In spite of their abundance, Clarkforkian phenacodontids are not diverse. This is consistent with Rose's (1981) conclusions that the Clarkforkian faunas in general have low diversities.

Ectocion osbornianus is by far the most abundant phenacodontid. Evolution of this lineage includes the decrease in frequency of presence of the metaconid of P_3 and the entoconid of P_4. Some size decrease in the early Clarkforkian also may occur, but samples are too small to document this adequately. Another Clarkforkian lineage is *Ectocion major.* This form is rare in the Bighorn Basin, but has been found in all three Clarkforkian biochrons. It is more abundant in the Piceance Basin of Colorado and differs from *E. osbornianus* mainly in its larger size. *Ectocion major* is not known from sediments younger than Clarkforkian.

E. parvus first appears in the late Clarkforkian. It is smaller than *E. osbornianus,* but the large samples currently available indicate that the two forms can only be distinguished on the basis of size characteristics. Only one specimen of *E. parvus* is known from the *Phenacodus-Ectocion* zone of the Bighorn Basin, but it is abundant in the *Cantius torresi* zone. *E. parvus* is also known from a single specimen of the Lower *Haplomylus-Ectocion* zone and is not found in younger deposits. *E. osbornianus* and *E. parvus* co-occur for all of the range of the latter, but there are large differences in their relative abundances. The larger *E. osbornianus* dominates in the *Phenacodus-Ectocion* and Lower *Haplomylus-Ectocion* zones, whereas smaller *E. parvus* dominates in the *Cantius torresi* zone. Kraus (1980) inferred from the lithologies of the Clarks Fork Basin that the sedimentary environment of the *Cantius torresi* zone differed from that in the zones over- and underlying it. Gingerich (1989) noted faunal differences between the *Phenacodus-Ectocion* zone and the *Haplomylus-Ectocion* zone on one hand, and the *Cantius torresi* zone on the other, and suggested that these differences could be the result of differences in the sedimentary environment. The co-occurrence of *E. osbornianus* and *E. parvus* does indicate that the latter is not a small, short lived ecophenotype of the former. The sedimentologic, stratigraphic, and faunal evidence suggests that *E. osbornianus* and *E. parvus*

are ecologically different, and that the pattern of their distribution is the result of these differences.

The smaller of the two Clarkforkian *Phenacodus* lineages is *Phenacodus vortmani*. There is no clear shape evolution in this lineage, although size may decrease during the Clarkforkian. The Buckman Hollow sample of this taxon has larger mesostyles than Clarkforkian Bighorn Basin *P. vortmani*, but this difference is based on few specimens, and its relevance cannot be evaluated until more material becomes available. *Phenacodus intermedius* is the largest Clarkforkian phenacodontid. It only differs in details from *P. grangeri*. Clarkforkian *P. intermedius* evolves to slightly larger mean sizes and also increases its range of size variation. This is especially apparent in the principal component analysis (Fig. 35), where the variability in scores on PC-1 nearly doubles.

There is no evidence of a lineage of *Phenacodus* larger than *P. intermedius* in the Clarkforkian. This could be partly the result of differences in preserved environments. Tiffanian *P. magnus* is usually found in coarse-grained sediments, whereas the main Clarkforkian localities are the mudstones of the Clarks Fork Basin. Few analogues of the Tiffanian coarse-grained quarry localities are known from the Clarkforkian. By contrast, Wasatchian *P. trilobatus* is known from mudstone localities, and would conceivably have been recovered in Clarkforkian rocks if it occurred in the Clarkforkian.

Wasatchian *P. intermedius* and *P. trilobatus* are closely related, they are similar in known shape variables, and mainly differ in size. The size distribution of the combined taxa is bimodal and the total size range approximately twice as large as in early Clarkforkian *P. intermedius*. Population densities of the Wasatchian taxa are inversely correlated throughout the stratigraphic section. The taxa apparently co-occur throughout their range and stratigraphic differences could be the result of differences in the preserved environment. The increase in variability of *P. intermedius*, towards the end of the Clarkforkian, the morphological similarity of this taxon with closely related Wasatchian *P. intermedius* and *P. trilobatus*, and the temporal and geographical continuity of the taxa suggest that the Wasatchian taxa are the outcome of cladogenesis in Clarkforkian *P. intermedius*. It is unclear what sparked the cladogenic event. The event apparently occurred during the *Cantius torresi* zone, and this suggests that the aberrant physical conditions of this zone (Gingerich, 1989) might be implied.

Copecion brachypternus first appears in the middle Clarkforkian. Few specimens are known from middle and late Clarkforkian, and the taxon is not known from the *Cantius torresi* zone. Smaller *Copecion davisi* is common in this zone in the Bighorn Basin. Gingerich (1989) noted that the *Cantius torresi* zone is characterized by the abundance of diminutive taxa. As pointed out before, there are indications that the fauna may represent a sample from a different environment than that of the *Phenacodus-Ectocion* and Lower *Haplomylus-Ectocion* zones. *C. davisi*

is also known from the Powder River Basin. The *Cantius torresi* zone is apparently environmentally different from pre- and postdating zones, but differences in the fauna are partly the result of temporal differences (Gingerich, 1989).

In short, habitat differences are not apparent between known Clarkforkian *Phenacodus*, although this could be due in part to the homogeneity of preserved environments. *Ectocion* and *Copecion* are represented by small taxa in the earliest Wasatchian. This is at least partly the result of differences in preserved environments.

Wasatchian and Bridgerian

Wasatchian phenacodontids are less abundant, but more diverse than Clarkforkian taxa. Wasatchian phenacodontids are morphologically similar to Clarkforkian forms, except for the unusual forms of the *Cantius torresi* zone that were discussed before.

Ectocion osbornianus from the Lower *Haplomylus-Ectocion* zone is slightly smaller than that from the Upper *Haplomylus-Ectocion* zone, but no shape changes are apparent. The taxon is not known from deposits postdating the Upper *Haplomylus-Ectocion* zone and was apparently restricted to northern latitudes. Its southernmost occurrence is in the Washakie and Piceance Basins, where it is less abundant than in northern areas of the same age.

The genus *Ectocion* is not known from the *Bunophorus, Heptodon,* and *Lambdotherium* zones, but reappears in the earliest Bridgerian (Krishtalka et al., 1987). *Ectocion superstes* is larger than *Ectocion osbornianus,* and it is only known from the *Palaeosyops* zone of the Wind River Basin.

No evolutionary trends are apparent in Wasatchian *Phenacodus vortmani*. The taxon is extremely rare in the Upper *Haplomylus-Ectocion* zone of the Bighorn Basin but it is abundant before and after that. The last *Phenacodus vortmani* are known from the Bridgerian. The geographic range of the taxon spans the Western Interior. It was apparently unconstrained by increasing seasonality in the Wasatchian.

Two lineages of large *Phenacodus* are known from the Wasatchian, *P. intermedius* and *P. trilobatus*. These taxa differ only in mean size, and their size ranges overlap. Evidence that two taxa are present comes from their changing abundances throughout the stratigraphic column, their absolute range of variation, and the shape of their size distribution.

Schankler (1981) described the pattern of phenacodontid evolution in a large part of the Wasatchian of the Bighorn Basin, and used ecological processes to explain many of the changes in abundance and diversity. Collections made since Schankler's work alter the pattern described by him in minor respects only (Fig. 51). *Ectocion osbornianus, Copecion brachypternus, Phenacodus vortmani,* and *P. intermedius* dominate in the Lower *Haplomylus-Ectocion* zone, while few specimens of *P. trilobatus* are known. *Copecion brachypternus* is not known from the Upper *Ha-*
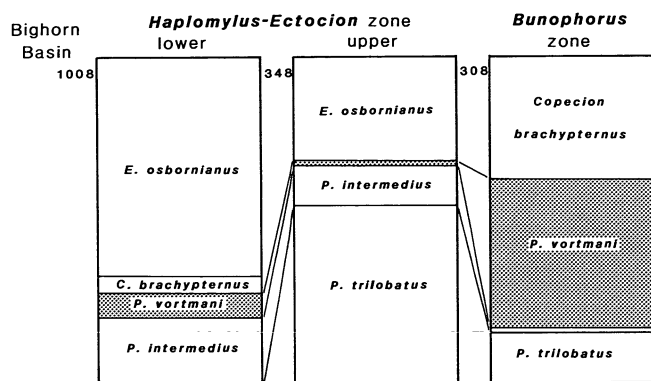
Figure 51. Temporal abundance shifts in Wasatchian phenacodontids from the Bighorn Basin. Lower *Haplomylus-Ectocion* zone is dominated by *Ectocion osbornianus* and *Phenacodus intermedius*. Upper *Haplomylus-Ectocion* zone is characterized by the absence of *Copecion brachypternus*, near absence of *P. vortmani* (stippling), and dominance of *P. trilobatus*. *P. intermedius* is abundant early in this zone, but rare later. *Bunophorus* zone is dominated by *C. brachypternus* and *P. vortmani*, and less common *P. trilobatus* and *P. intermedius* (unlabeled bar). Numbers near left upper corner of bars represent numbers of specimens from each bar.

plomylus-Ectocion zone, and *Phenacodus vortmani* is very rare here (no specimens were known to Schankler; unlabeled bar in Fig. 51). *Phenacodus intermedius* is known from the earlier part of the Upper *Haplomylus-Ectocion* zone, but not from the later part. *P. trilobatus* is common in the Upper *Haplomylus-Ectocion* zone. The end of the Upper *Haplomylus-Ectocion* zone brings the extinction of *Ectocion osbornianus*. *C. brachypternus* and *P. vortmani* return as dominant phenacodontids in the *Bunophorus* and *Heptodon* zones, whereas *P. intermedius* (unlabeled bar in Fig. 51) and *P. trilobatus* are present but rare.

Schankler (1981) described a general decline of phenacodontids over the course of the Wasatchian and suggested that it was caused by competition between perissodactyls and phenacodontids. The sharp decline in the relative abundance of phenacodontids from Clarkforkian to early Wasatchian faunas has been documented in detail by Rose (1981) and Gingerich (1989), but that does not directly support Schankler's scenario. Data on the relative abundance of phenacodontids and perissodactyls can be used to address the question of competition, but such data are unavailable at present for all of the Wasatchian. Successive early Wasatchian samples from the Clarks Fork Basin are approximately 30,000 years apart in time (Gingerich, 1983). Comparison of faunal composition level by level can be used to investigate the competition hypothesis if phenacodontids were gradually replaced by perissodactyls in time intervals of the order of magnitude of 10,000 years in the Lower *Haplomylus-Ectocion* zone. Data from University of Michigan collections for the Clarks Fork Basin were used to test Schankler's proposal for the early Wasatchian.

Gingerich (1989) studied faunal succession across the Clarkforkian-Wasatchian boundary with principal component analysis. This method can also be used to study Schankler's competition hypothesis for the Lower *Haplomylus-Ectocion* zone. I analyzed 52 Wasatchian levels from the Clarks Fork Basin. The analyzed variables for each level were the number of specimens of eight common genera: *Hyracotherium, Homogalax, Diacodexis, Cantius, Hyopsodus, Phenacodus, Ectocion,* and *Copecion*. Principal component analysis could show patterns of correlation among the abundance of these common taxa. The outcome would form a critical test of Schankler's competition hypothesis if increase of perissodactyls and decrease of phenacodontids consisted of a gradual replacement of phenacodontids by perissodactyls, and if this affected faunal composition in a major way. Strong negative correlation between the perissodactyl *Hyracotherium* and the phenacodontid *Ectocion* was found in principal component 3 (Table 9), but it explained only .82% of the total variance. The scores of time-ordered levels of PC-1 did not show a trend (Fig. 52). I conclude that abundances of phenacodontids and perissodactyls are not strongly correlated in the early Wasatchian of the Clarks Fork Basin, and that this is inconsistent with gradual replacement of phenacodontids by perissodactyls, a possible mechanism in Schankler's (1981) competition hypothesis.

Principal Component 2 explained 3.3% of the total variance. Loadings indicate that high abundances of *Hyopsodus* are correlated with low abundances of *Hyracotherium* and *Ectocion*. One possible explanation for this inverse correlation is differences in sampled environments. Levels with abundant *Hyopsodus* represent samples from different environments than levels with abundant *Hyracotherium* and *Ectocion*.

Schankler (1981) proposed that increased competition with *Ectocion* caused the rarity of *P. vortmani* and *C. brachypternus* in the Upper *Haplomylus-Ectocion* zone, and that the cause of the shift in dominance was the result of changing environments. Badgley and Gingerich (1988) have shown that a similar shift in the Clarks Fork Basin could be an artifact of decreased sample sizes. This alternative explanation may not hold in the area studied by Schankler (1981), the central Bighorn Basin.

Important shifts in the abundance of *Phenacodus* lineages also occur early in the Upper *Haplomylus-Ectocion* zone. *C. brachypternus, P. vortmani,* and *P. intermedius* decrease in numbers, and *P. trilobatus* becomes common. All these taxa, except *C. brachypternus*, are known from both the Lower and Upper *Haplomylus-Ectocion* zones; the shifts in dominance apparently reflect long-term changes rather than subsequent extinctions and introductions. The pattern of these changes echoes that of the late Tiffanian: in both cases large *Phenacodus* (Tiffanian *P. magnus* and Wasatchian *P. trilobatus*) replace two smaller taxa (Tiffanian and Wasatchian *P. vortmani;* Tiffanian *P. grangeri,* and Wasatchian *P. intermedius*). As pointed out before,

Table 9. Principal component loadings for faunal analysis of early Wasatchian.

Taxon	PC-1	PC-2	PC-3
% of variance	94.9	3.3	0.8
Hyopsodus	0.83	−0.46	−0.06
Hyracotherium	0.39	0.69	−0.59
Cantius	0.33	0.05	0.47
Diacodexis	0.21	0.25	0.34
Ectocion	0.10	0.49	0.54
Homogalax	0.04	−0.09	−0.10
Phenacodus	0.03	−0.01	−0.10
Copecion	0.01	0.02	0.01
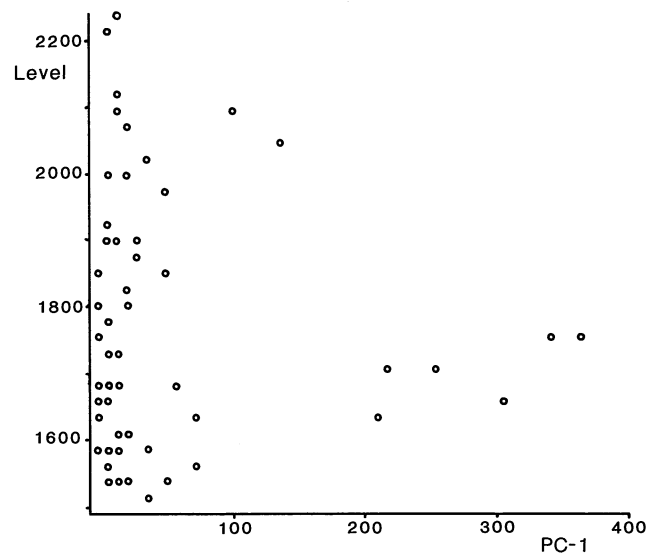
Figure 52. Scores on principal component 1 for subsequent levels in the Clarks Fork Basin section. See text for explanation.

sedimentological evidence supports the role of sedimentary facies in determining abundance in Tiffanian phenacodontids. The Wasatchian pattern may have had a similar cause. Using the sedimentary environment of the Tiffanian as an analogue, one could argue that the presence of very large *P. trilobatus* of the Upper *Haplomylus-Ectocion* zone indicates near-channel sedimentary environment. This might contrast the well-drained floodplains of the Lower *Haplomylus-Ectocion* zone, where *P. vortmani* and *P. intermedius* dominated. These inferences can be tested through the study of the lithology of the mudstone deposits in which the fossils are found (Bown and Kraus, 1987).

P. vortmani is the only common phenacodontid of the *Bunophorus* zone, and few phenacodontid specimens are known from the *Heptodon* and *Lambdotherium* zones. Bridgerian phenacodontids are very rare, although the family does not go extinct until the second half of that age.

EUROPEAN PHENACODONTIDAE

European phenacodontids are poorly known, and never attain the abundances known from North America. Based on available evidence, European *Phenacodus* differ from North American forms mainly in having a short dentary,

possibly with a fused mandibular symphysis. European phenacodontids are known from the early and middle Eocene (Dormaalian through Robiacian). Only tentative comparisons can be made between North American and European *Phenacodus*, because sample sizes of European taxa are small. Gingerich (1989) correlated Dormaalian faunas from Europe to Wasatchian faunas from North America. A *Phenacodus* specimen from the earliest Wasatchian of the Bighorn Basin (UM 83622, figured by Gingerich, 1989) was identified in the previous chapter as *P. vortmani*. P_4 of this specimen is relatively larger than other North American *P. vortmani*, whereas European *P. lemoinei* have premolars that are typically smaller than *P. vortmani*. On the other hand, UM 83622 has a short jaw with few diastemata, similar to the few mandibulae known for European *Phenacodus*, but unlike other North American *Phenacodus*.

The earliest Eocene locality Dormaal has yielded small *Phenacodus teilhardi*. *P. teilhardi* is the only phenacodontid at Dormaal, but *P. lemoinei* is known from the contemporaneous fauna of Pourcy. *P. lemoinei* is also known from localities that postdate *P. teilhardi*. No European phenacodontids are known from the Geiseltalian, but *Phenacodus condali* is known from younger rocks. *Phenacodus condali* is larger than the other European taxa.

V

CRANIAL OSTEOLOGY OF THE PHENACODONTIDAE

Cope (1885) was the first to describe cranial and postcranial osteology of phenacodontids. He discussed skulls and skeletons of *Phenacodus vortmani* (AMNH 4378) and *Phenacodus intermedius* (AMNH 4369) extensively, and his ideas about the relationships of mammals were to a large extent based on his observations on these skeletons. Osborn (1898b), Kitts (1956) and Radinsky (1966) made additional observations on the osteology of these taxa, and Gazin (1956c) figured a rostrum of *Ectocion mediotuber* (USNM 20736). Cope (1882d), Simpson (1933), and Radinsky (1976) described the endocast of *Phenacodus* (AMNH 4369). I will describe the skull of a specimen of *Phenacodus intermedius* for which Cifelli (1982) described the petrosal region (PU 14864). Matthew (1897), Osborn (1898b) and Radinsky (1966) provide descriptions of the osteology of *Tetraclaenodon puercensis,* for which fragmentary skeletons and few cranial remains are known.

In this chapter, I will discuss previously undescribed cranial material of three phenacodontids: *P. intermedius, P. vortmani,* and *Ectocion osbornianus.*

MATERIAL

The skull of *Phenacodus intermedius* is described on the basis of a specimen in the Princeton exhibit collection (PU 14864, locality data listed in discussion of *P. intermedius*). This specimen (Fig. 53) is in near perfect condition, only small fragments of the zygomatic arches, the left nasal and left nuchal crest are missing. Deformation is limited to the slightly cracked palate. In addition, I have studied a crushed skull with well preserved basicranial region (UM 73017; from UM locality SC-63 in the Bighorn Basin, Upper *Haplomylus-Ectocion* zone).

Phenacodus vortmani is represented by a skull from the *Heptodon* zone of the Bighorn Basin (YPM 20524; YPM locality 16). This specimen (Fig. 54) lacks zygomatic arches, parts of the orbital rim, left nasal, and left retroarticular and mastoid process. Part of the left wall of the braincase has been removed, and the endocast shows here. Many large cracks are present and the palate is crushed and distorted posteriorly.

The best preserved skull of *Ectocion osbornianus* was found in the *Plesiadapis cookei* zone (UM 86155, UM locality SC-29). This specimen (Fig. 55) lacks part of the right nasal, the anterior parietals, the left lacrimal, the left

zygomatic arch and the posterior part of the right zygomatic arch. The posterior part of the braincase that houses the cerebellum is missing, and only fragments of the basicranium remain. The individual was young, D^3 and all molars are erupted, D^4 is missing, and P^4 is erupting. Lateral compression has deformed the palate and pterygoid region. Remnants of the hyoid arch are also preserved in this specimen, as well as the dentaries and axis. An additional cranial specimen of *Ectocion osbornianus* is UM 69679 (UM locality SC-62, *Plesiadapis cookei* zone). This specimen consists of a badly crushed skull, which retains a well preserved occipital region, petrosals, and left mandibular fossa.

DESCRIPTION

Overall morphology.—*Phenacodus intermedius* has a massive skull with large nasal openings and inflated frontal area. This inflation appears to be absent in another specimen of *P. intermedius,* judging from Cope's (1885) description and figures. The rostrum of *P. intermedius* is long, there are diastemata between all cheek teeth anterior to P^3. *Phenacodus vortmani* is smaller and similar in overall shape, but lacks large nasal openings and inflated frontals. It has a shorter rostrum and there are no diastemata between canine, P^1 and P^2. *Ectocion osbornianus* has a small skull and a long, narrow rostrum. The nasal opening is small and the frontals uninflated, but the lacrimals and antorbital part of the frontals are enlarged.

The skull of *Ectocion* is more elongate than that of *Phenacodus.* The orbit of *P. intermedius* reaches as far anterior as M^2, whereas in *P. vortmani* and *Ectocion* it reaches to M^1. The braincase of all three phenacodontids is smaller than the nasal cavity, the sagittal and nuchal crests are similar in size and shape in the two *Phenacodus* specimens. The sagittal crest of *Ectocion* is weaker and nuchal crests are not preserved. A partial auditory bulla is only preserved in *Ectocion.* The retroarticular process is larger than the mastoid and jugular processes.

Premaxilla.—The premaxilla is wide rostrally and narrow caudally in anterior view. Its caudal process ascends to form the lateral border of the nasal opening in *P. intermedius.* The rostral and caudal parts are more similar in robustness in *P. vortmani* and *Ectocion* than in *P. intermedius.* Dorsally, the nasal process of the premaxilla ends in
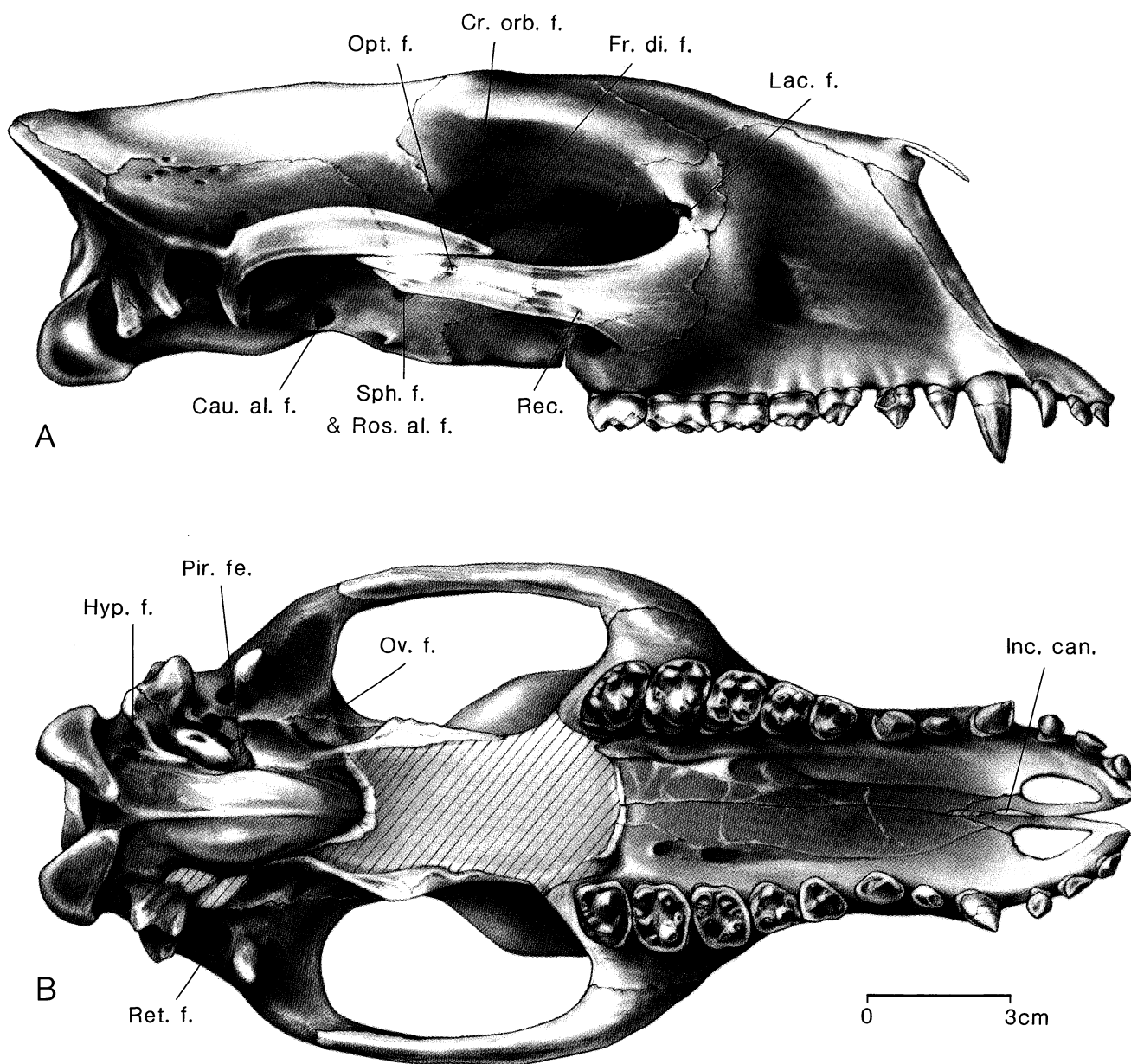
Figure 53. A and B, Skull of *Phenacodus intermedius* (PU 14864), lateral and ventral view. Zygomatic arch is indicated as if transparent in order to show structures of orbit. Cau. al. f., caudal alar foramen; Cr. orb. f., cranio-orbital foramen; Fr. di. f., frontal diploic foramen; Hy., fragments of hyoid bones; Hyp. f., hypoglossal foramen; Inc. can., incisive canal; Lac. f., lacrimal foramen; Opt. f., optic foramen; Pir. fe., piriform fenestra; Pos. tor., postpalatine torus; Ov. f., oval foramen; Pter. ham., pterygoid hamulus; Rec., recess for sphenopalatine and posterior palatine foramina; Ret. f., retroarticular foramen; Ros. al. f., rostral alar foramen; Sph. f., sphenorbital fissure.

a projection between the maxilla and nasal in all three skulls. The rostral extremities of the bilateral premaxillae are not juxtaposed in *Phenacodus*. This region is not preserved in *Ectocion*.

On the palate, the premaxilla extends posteriorly between the maxillae in all three phenacodontids. The pre-

maxillae form the lateral, rostral, and medial borders of the palatine fissures, and enclose the incisive canal posterior to this. The suture between premaxilla and maxilla crosses a shallow fossa that houses the lower canine when the mouth is closed. This fossa is deeper in *Ectocion* than in *Phenacodus*.
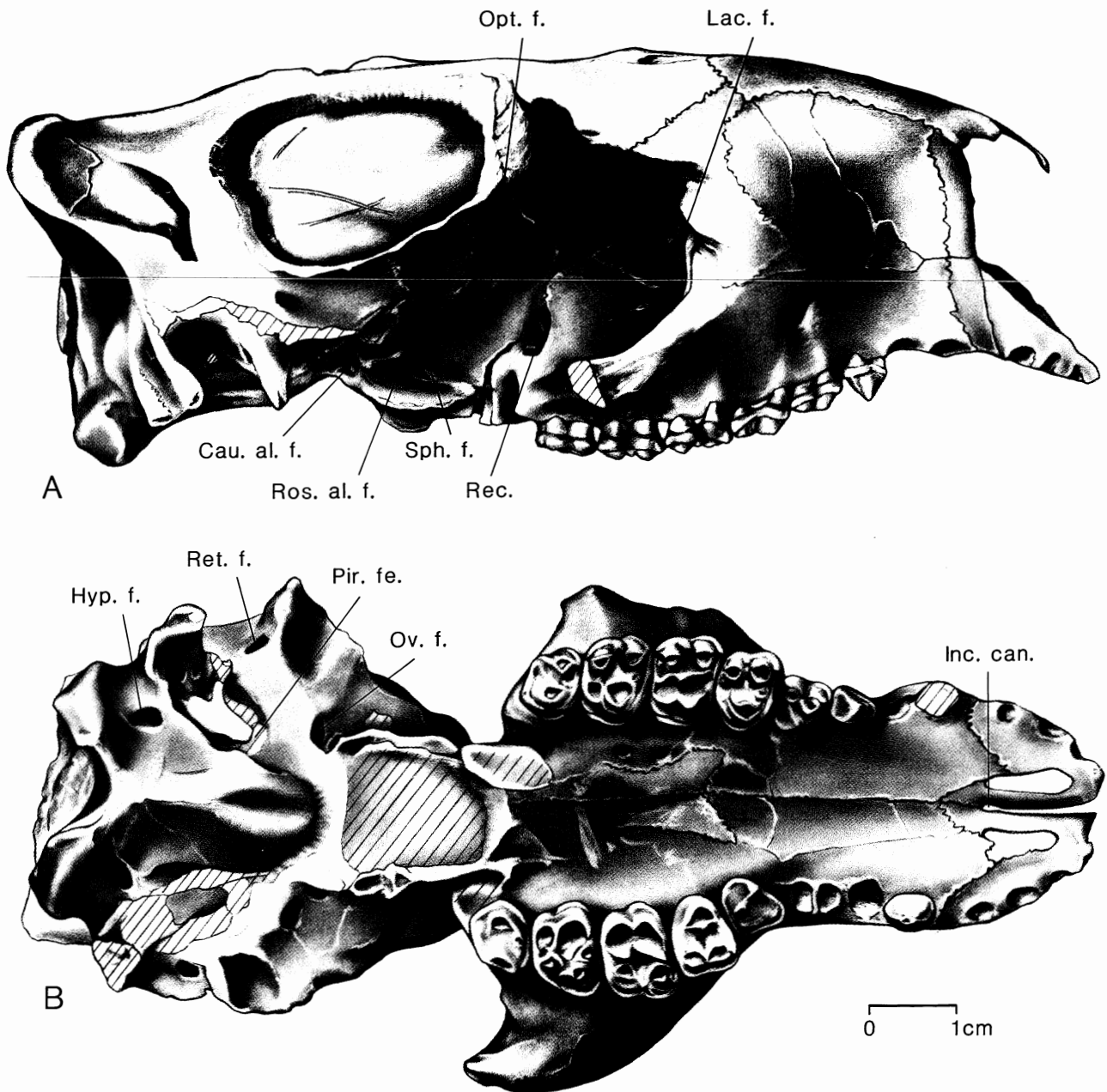
Figure 54. A and B, Skull of *Phenacodus vortmani* (YPM 20524), lateral and ventral view. Abbreviations as in Fig. 53.

Nasal bone.—The rostral tip of the nasal projects anteriorly in all three skulls. The tip of the nasals of *P. intermedius* is over C^1, it is over I^2 in *P. vortmani*. The edge extends laterally and posteriorly to the level of P^2, where it bends rostrally and forms a process in *Phenacodus*, but not in *Ectocion*. The nasal narrows posteriorly at its contact with the maxilla, until it reaches the level of the anterior orbit. The nasal is broader posterior to this point and it has a broad contact with the frontal.

Maxilla.—The maxilla shares sutures with the premaxilla, nasal, lacrimal and zygomatic on the face of all phenacodontids. No contact with the frontal is present, and the
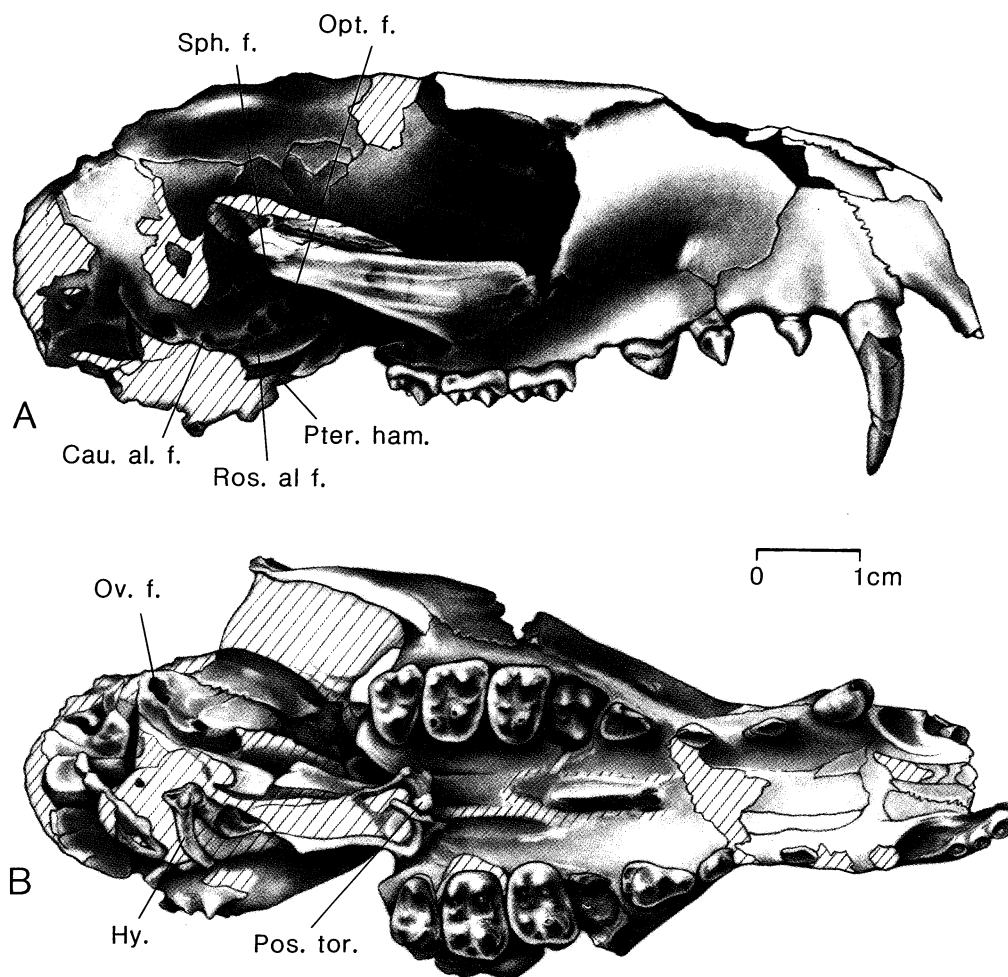
Figure 55. A and B, Skull of *Ectocion osbornianus* (UM 86155), lateral and ventral view. Abbreviations as in Fig. 53. Notice difference in canine length of this presumed male with presumed female of fig. 18.

maxilla does not contribute to the orbital rim. The anterior opening of the infraorbital canal is dorsal to M^1 in *Phenacodus intermedius*, but more rostral in *P. vortmani* and *Ectocion*. The foramen is larger, and its canal shorter in *P. intermedius* than in the other phenacodontids.

The maxillae are deeply bisected by the premaxillae on the palate in *Phenacodus* and *Ectocion*. One large and one small palatine foramen are medial to the molars in *P. intermedius*, and in the other two skulls several foramina of approximately equal size are present in this area. The orbital process of the maxilla is limited to the floor of the orbit; its suture with the palatine is long and extends anteroposteriorly. There is no maxillary tubercle in any phenacodontid.

Zygomatic bone.—The zygomatic forms the lower third of the orbital rim. It has a short contact with the lacrimal and a longer, more or less straight contact with the maxilla.

The zygomatic arch is only preserved in *P. intermedius;* the zygomatic bone has a horizontal contact with the squamosal and extends posteriorly to the anterior edge of the mandibular fossa.

Palatine bone.—The notch in the posterior palate for the minor palatine neurovascular group is oriented vertically. It is deep, and its medial wall is formed by the palatines. A postpalatine torus is present in *Ectocion*.

The orbital process of the palatine extends rostrally and forms a wedge between the lacrimal and maxilla. The palatomaxillary suture extends horizontally in *Phenacodus intermedius*, but it extends obliquely dorsoventral in *P. vortmani*. In *Ectocion* this region is disturbed. The palatine is enlarged in the posterior part of the orbit of *Phenacodus*, and forms a large part of the pterygoid wing. The recess housing sphenopalatine and caudal palatine foramina is on the suture with the maxilla in *Phenacodus*. The spheno-

palatine foramen is larger than the caudal palatine foramen. This area is not preserved in *Ectocion*.

Lacrimal bone.—The lacrimal articulates with the zygomatic, maxilla, and frontal on the face. In *Phenacodus* it articulates with the frontal and palatine in the orbit, whereas no sutures are visible in the anterior orbit of *Ectocion*. A lacrimal tubercle is present in *Phenacodus*, but not in *Ectocion*. The lacrimal foramen opens into the orbit ventral to the lacrimal tubercle. A notch in the orbital rim of *P. intermedius* opens over the lacrimal foramen, while in *P. vortmani* and *Ectocion* a groove extends dorsally from the foramen within the orbit.

Pterygoid bone.—The suture between pterygoid and palatine is obliterated in all three skulls. The pterygoid hamulus is strong in *Ectocion*, and lateral to it is the fossa for the medial pterygoid muscle. The hamulus is broken, but the fossa is still recognizable in *P. vortmani*. There is no fossa in *P. intermedius*, although the area of origin of the medial pterygoid is rough. The pterygoid extends as far posteriorly as the caudal alar foramen in *P. intermedius*.

Frontal bone.—The frontal shares sutures with nasal, lacrimal, palatine, orbitosphenoid and parietal. The dorsal side of the frontal, which houses the frontal sinus, is inflated in *P. intermedius*, but not in the other phenacodontids. The suture with the parietal extends caudolaterally from the median plane, and bends rostroventrally towards the orbitosphenoid. Its most ventral extension is posterior to the cranio-orbital foramen. This foramen is at the edge of a elevated rough area for the origin of the ventral part of the temporal muscle. The cranio-orbital foramen is elongated dorsoventrally and constricted between the extremities. Anterior to it is the foramen for the frontal diploic vein (Thewissen, 1989). Two sulci extend from the latter, one anteriorly, and another caudoventrally to the ventral part of the cranio-orbital foramen. The ventral part of the cranio-orbital foramen probably admitted the lateral cerebral sinus, and the dorsal part may have emitted an artery. The frontal suture extends ventral to the frontal diploic foramen and bends dorsally at the level of the sphenopalatine foramen. The frontal suture of *P. vortmani* cannot be followed, but cranio-orbital and frontal diploic foramina are present and more ventrally directed than in *P. intermedius*. The cranio-orbital foramen of *P. vortmani* is disproportionately smaller than in *P. intermedius*. The frontal diploic foramen of *Ectocion* opens in the postorbital process, and not in the ventral part of the orbit. The ventral part of the frontal is distorted in *Ectocion*, but the cranio-orbital foramen appears to be absent. The orbitotemporal crests of *Ectocion* and *P. vortmani* are more laterally directed than in *P. intermedius*, and the postorbital process is stronger in *P. vortmani*.

Parietal bone.—The parietals form the posterior part of the temporal lines and the sagittal crest. This crest is weaker in *Ectocion* than in *Phenacodus*. The parietal projects between frontal and squamosal anteroventrally. The parietosquamous suture and adjacent areas of both bones are perforated by numerous small foramina. The suture reaches the nuchal crest halfway between its ventral and dorsal extremities and bends dorsally. The sutures of the parietal are not preserved in *Ectocion*.

Sphenoid bones.—No sutures are visible between the sphenoid bones in any of the specimens. The optic foramen is ventral to the cranio-orbital foramen, and the sphenorbital fissure opens with the rostral alar foramen in a broad depression caudoventral from the optic foramen in *P. intermedius*. The sphenorbital fissure and the rostral opening of the alar canal are well separated in *P. vortmani* and *E. osbornianus*. No round foramen is visible on the skulls, and judging from the endocasts described by Cope (1882d) and Simpson (1933), it is fused to the sphenorbital fissure. The caudal alar foramen is anterior to the oval foramen in *P. intermedius*, but anteromedial in *Ectocion* and *P. vortmani*. The alisphenoid of *P. intermedius* is grooved for the internal carotid artery posterior to the oval foramen. Two small vascular foramina flank the oval foramen of *P. intermedius* (PU 14864) on the right side, and only one on the left side. No vascular foramina are present in another specimen of *P. intermedius* (UM 73017) or in *P. vortmani* and *Ectocion*.

The suture between sphenoid and temporal extends from the piriform fenestra (sensu MacPhee, 1981) to the edge of the elevated area of the parietal, where it bends dorsally to the cranio-orbital foramen and then ventrally to the optic foramen. It cannot be followed farther anteriorly. The suture between sphenoid and pterygoid extends along the root of the pterygoid process in *P. intermedius* and cannot be followed in *P. vortmani* and *Ectocion*.

The anterior edge of the piriform fenestra bears medial and lateral notches for the internal carotid artery and musculotubal canal. The pterygoid groove extends from the medial notch to the pterygopalatine fossa but cannot be traced anteriorly in *P. intermedius*.

Occipital bone.—The occipital is not preserved in *Ectocion*. In *Phenacodus*, the occipital forms part of the skull roof adjacent to the sagittal plane. The occipital forms the dorsal part of the nuchal crests, while the squamosal forms the ventral part. The occipital side of the nuchal crests is rugose for muscle attachment and perforated by a few venous foramina. A single large foramen occurs on the suture between mastoid and occipital in *P. intermedius*, but not in *P. vortmani*.

The occipital condyles are well separated ventrally. Lateral to the occipital condyles is the jugular process. The hypoglossal foramen is present. The basioccipitals are elevated for the insertion of rectus capitis ventralis.

Temporal bone.—The squamous part of the temporal bone forms the large, more or less flat mandibular fossa, as well as a small part of the wall of the cranial cavity. Here, it is perforated by several foramina in all three phenacodontids.

The suture between sphenoid and squamosal extends more or less anteroposteriorly. The retroarticular process is present posterior to the retroarticular foramen. Posterior

to it, the squamosal forms the roof of the external auditory meatus, and it articulates with the mastoid on the occipital aspect of the skull.

The opening of the external auditory meatus has the shape of a half circle in *Ectocion*. Fragments of ectotympanic and hyoid arch are also preserved. The ectotympanic forms an osseous bulla that covers the middle ear cavity at least partly. Only the lateral part, approximately 4 mm, of the bulla is preserved. It is slightly convex and would have covered approximately the lateral two thirds of the middle ear cavity. The medial part of the ectotympanic is not preserved.

The petrosal part of the temporal was described in detail by Cifelli (1982) for *Phenacodus intermedius,* and little can be added to his description. One of the few points of disagreement between Cifelli's and my interpretation of the petrosal region concerns the presence of a sulcus for the stapedial artery. I am not convinced that the structure indi-

cated in Cifelli's figure 3 is the stapedial sulcus. This area is irregular in texture and not depressed in two specimens of *Phenacodus intermedius* available to me (PU 14864 and UM 73017). The stapedial sulcus is typically smooth and depressed, and it is thus unclear whether it was present in *Phenacodus*.

A slit-like depression extends from the medial side of the petrosal over the cochlear window in a specimen of *Ectocion* (UM 69679) and bends posterior to the fossa for the stapedial muscle. It does not extend to the vestibular window and has an irregular surface. The sulcus is therefore probably not for the stapedial artery.

Dentary.—Radinsky (1966) described the shape of the dentary of *Phenacodus* and *Ectocion*. The angular process of *Ectocion cedrus* (YPM-PU 21251) and *E. osbornianus* (UM 65381) is larger than that figured by Radinsky (1966). The angular process is hook-shaped in these specimens.

VI
NOTES ON THE POSTCRANIAL OSTEOLOGY OF PHENACODONTIDAE

Skeletons of *P. intermedius* and *P. vortmani* have been studied by paleontologists for over a hundred years (Cope, 1885; Matthew, 1897; Osborn, 1898b; Kitts, 1956; Radinsky, 1966). Here, I will not redescribe or reinterpret all of phenacodontid postcranial anatomy, but instead focus on a partial skeleton of a taxon for which no postcranials have been described previously, *Copecion brachypternus*.

I will compare phenacodontid postcranials of *Copecion brachypternus* with those of *Phenacodus vortmani*, *P. intermedius*, *P. trilobatus*, *Ectocion osbornianus*, and *Copecion davisi*. New skeletal material of *Ectocion* and *Copecion davisi* is very incomplete, whereas more or less complete material for the *P. vortmani* and *P. intermedius* has been described by previous authors.

MATERIAL

The description of *Copecion brachypternus* is based on a specimen from the *Bunophorus* zone of the central Bighorn Basin (UM 64179; UM locality YM-421; Fig. 56), which includes dental material, vertebral fragments and complete sacrum, distal scapula, left humerus lacking lateral condyle, proximal and distal right humerus, left proximal radius, fragments of both proximal ulnae, complete left femur, patella, both tibiae, proximal fibula, both astragali and calcanei, navicular, cuboid, one complete metapodial and distal fragments of two others, and a phalanx.

Comparisons with *Ectocion osbornianus* are mainly based on two specimens. The first of these is from the Lower *Haplomylus-Ectocion* zone of the Clarks Fork Basin (UM 83100; UM locality SC-210). It includes dental material, damaged proximal half of a humerus, proximal radius and ulna, distal ulna, fragments of os coxae and proximal femur, distal femur, nearly complete tibia, calcaneus, and a few phalanges. The second specimen comes from late Clarkforkian rocks of the Clarks Fork Basin (UM 65089; UM locality SC-24). It includes a distal right humerus and both proximal ulnae, as well as proximal and distal radius and femoral head.

Among the most important additional phenacodontid postcranials are partial skeletons of *Phenacodus vortmani* (UM 75286 from UM locality GR-9; *Bunophorus* zone of the central Bighorn Basin), *P. intermedius* (UM 93237 from UM locality SC-234; *Plesiadapis cookei* zone of the Clarks Fork Basin), *P. trilobatus* (UM 82241, UM locality

SC-54; UM 94050, UM locality MP-166; UM 94232, UM locality MP-172; UM 94330, UM locality MP-175; all Wasatchian of the Clarks Fork and Bighorn basins) and some postcranials of *Copecion davisi* (UM 66611 from UM locality SC-67; *Cantius torresi* zone of the Clarks Fork Basin).

DESCRIPTION

Clavicle.—A clavicle has never been described for a phenacodontid, but a fragment of the bone is preserved in a specimen of *P. vortmani* (UM 75286). It consists of the sternal joint and a fragment of the shaft (Fig. 57). The cross section of the sternal extremity of the shaft is oval and bears a rugose area for the origin of the clavicular head of sterno-cleidomastoid. Laterally, the shaft widens, flattens and is more triangular in cross section.

Scapula.—Only the distal part of the scapula is preserved in *C. brachypternus* and *Ectocion*. The glenoid cavity is oval anteroposteriorly, and the coracoid process is somewhat medially deflected as in all phenacodontids. The supraglenoid tubercle is stronger in *Copecion brachypternus* than in other phenacodontids (*Ectocion*, UM 91426; *Phenacodus vortmani*, UM 75286; *Phenacodus trilobatus*, UM 94330). The suprascapular notch of the scapula is weak in *Copecion* and *Phenacodus intermedius* (PU 14864). The root of the acromion is far posterior on the scapula in *Copecion* and *Phenacodus* (UM 75286).

Humerus.—The greater tubercle of the humerus is nearly as large as the humeral head in *Copecion* (UM 64179) and *Phenacodus* (*P. vortmani*, USNM 16691; *P. trilobatus*, UM 82241). The lesser tubercle is disproportionately smaller, and the intertubercular groove is deep and wide. In *Ectocion osbornianus* (UM 91426) the greater tubercle is smaller and the intertubercular groove narrower than in *Phenacodus* and *Copecion*. The humeral head is equally convex anteroposteriorly and mediolaterally in *Copecion*, *Ectocion* and *P. vortmani*, but the head is mediolaterally flattened in *P. trilobatus*. The deltopectoral crest is essentially absent in *Copecion brachypternus* and *Ectocion* but present on the humerus of *Tetraclaenodon* (Matthew, 1897) and *Phenacodus* (*P. vortmani*, USNM 16691; *P. intermedius*, UM 66861; *P. trilobatus*, UM 94050). The medial epicondylar foramen and supracondylar foramen are present in *Copecion* as well as in other phenacodontids (*Ec-*
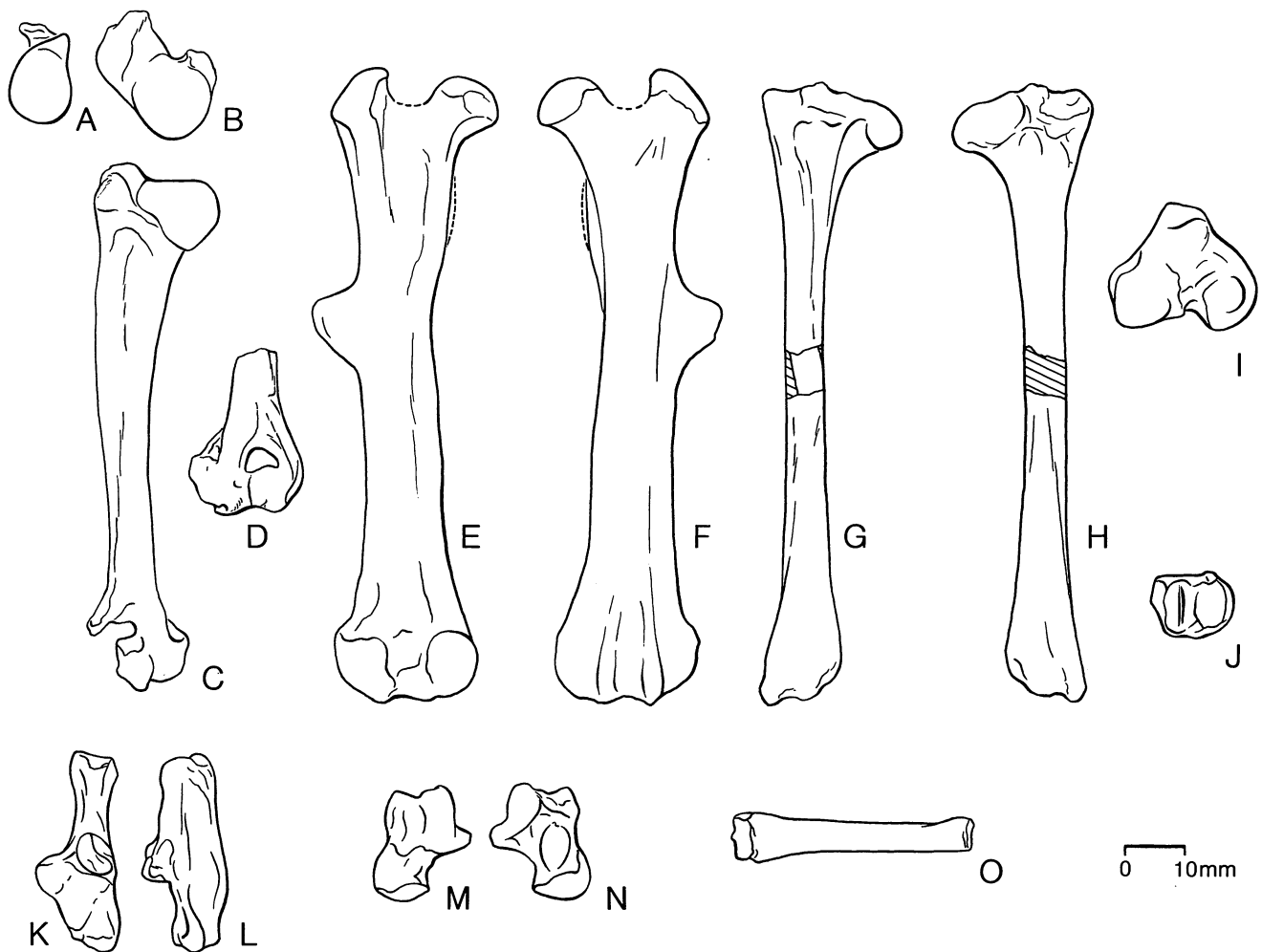
Figure 56. Postcranial osteology of *Copecion brachypternus* (UM 64179). A, scapula, distal view. B and C, left humerus, proximal and posterior view. D, distal right humerus, anterior view. E and F, left femur, posterior and anterior view. G through J, right tibia (two fragments), anterior, posterior, proximal, and distal view. K and L, left calcaneus, dorsal and lateral view. M and N, left astragalus, dorsal and plantar view. O, Metatarsal III?, dorsal view.

tocion, UM 65089; *P. vortmani*, UM 75286; *P. intermedius*, UM 93237; *P. trilobatus*, UM 94050) as noted by Cope (1882b).

Radius.—The proximal radius of *Copecion, Ectocion* (UM 65089), and *Phenacodus vortmani* (UM 75286, USNM 16691) is more or less oval in outline, but the proximal articular surface has a lateral process that articulates with the most lateral portion of the capitulum of the humerus. The process is absent in *Phenacodus trilobatus* (UM 94050). The joint for the ulna in phenacodontids extends along the entire posterior border of the radius.

Distally, the radius has joints for the scaphoid, lunar, and ulna in *Phenacodus* (UM 80254) and *Ectocion* (UM 65083). The joints for the two carpals are both concave mediolaterally as well as anteroposteriorly. The joint for the ulna is irregular. It is on the lateral side of the distal radius.

Ulna.—The olecranon is straight in *Copecion, Ectocion* (UM 65089), and *Phenacodus* (UM 94050, UM 75286). The semilunar notch is asymmetrical in phenacodontids.

The distal ulna of *Phenacodus* articulates with the cuneiform by means of a convex joint that mainly extends anteroposteriorly. The distal part of the shaft of the ulna has a blunt process anteriorly in *Copecion* and *Phenacodus* (UM 94330).

Carpus.—The carpus of *Phenacodus* was described in detail by Cope (1885). Cope used patterns of articulation between the carpals as important evidence to determine the phylogenetic relationship of the orders of mammals (e. g., Cope, 1882e, 1882h). Most authors have distinguished two

A

0   5 mm

B

Nutrient foramen
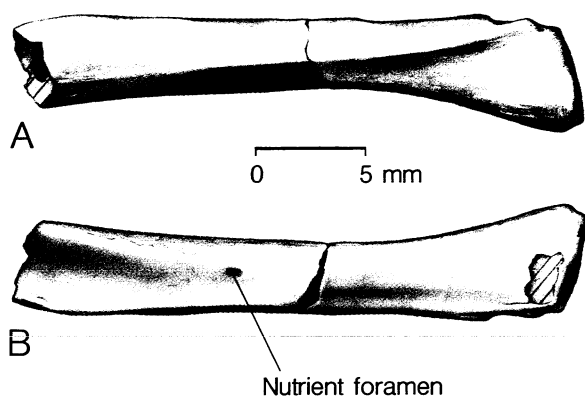
Figure 57. Clavicle of *Phenacodus vortmani* found in association with teeth and partial postcranial skeleton (UM 75286). Sternal joint on right. A, caudal view; B, cranial view.

main arrangements of carpal bones, serial and alternating. These terms are ambiguous. Cope usually described alternating to mean that the scaphoid "rests on" (1882h:439) the magnum, and that the lunar "rests on" the unciform. Cope (1882e) implied that the serial carpus lacks a facet for the scaphoid on the magnum, or for the lunar on the unciform. But Cope (1885) described *Phenacodus intermedius* as having both these facets and still considered the taxon serial, apparently because the proximal carpals do not "rest on" the distal ones. This blurs the difference between the two states, the carpal ligaments may transmit impact laterally as well as distally, and the absence of a contact between scaphoid and magnum in anterior view does not mean that such a contact is not present in a more palmar plane and that the carpus is not functionally identically to an alternating carpus.

I have not studied the carpus described by Cope (the specimen is on exhibit in the American Museum, and its carpus is set in plaster; W. Sanders, pers. comm., 1989), but a scaphoid-magnum and a lunar-unciform joint are present on the carpals of a composite *Phenacodus intermedius* (YPM-PU 13208). The contact between scaphoid and magnum is small in this specimen, but the facet between lunar and unciform is large and horizontal. The unciform therefore supported a large portion of the force exerted on the lunar, similar to the alternating carpus.

Matthew (1897) described joints between scaphoid (or centrale) and magnum, as well as between lunar and unciform in *Tetraclaenodon* (his *Euprotogonia*), and listed *Tetraclaenodon* as "non-serial" (p. 320). The difference in terms used for *Tetraclaenodon* and *Phenacodus* together with the assumption that the former is ancestral to the latter, led Osborn (1898a) to conclude that *Phenacodus* was "secondarily serial" (p. 175). Radinsky (1966) noted that there is a contact between the lunar and unciform in *P. vortmani*. Based on my observations and the published descriptions, I doubt that there are important differences in

the arrangement of the carpals between different phenacodontids.

Sacrum.—The sacrum of *Copecion brachypternus* consists of four vertebrae, as in *Phenacodus trilobatus* (YPM-PU 13208). The wing of the sacrum of *Copecion* is larger than that in *Phenacodus trilobatus*.

Os coxae.—The os coxae of *Copecion* (UM 64179) is slender and has a larger obturator foramen than *Phenacodus intermedius* (UM 93237). The cross section of the posterior ilium is more or less flat dorsoventrally in *Copecion* and *Phenacodus intermedius* (UM 93237), whereas in *P. trilobatus* (UM 94050) it is more triangular. This is mainly the result of the more vertical position of the surface from which the iliacus muscle originates. The ischial tuberosity of *Copecion* is stronger than that in *Phenacodus trilobatus* (YPM-PU 13208), and the ischial spine is large in both.

Femur.—The femur of *Copecion* resembles that of *Phenacodus intermedius* (UM 93237) and *P. trilobatus* (UM 82241) in overall shape. The greater trochanter is large and the lesser trochanter is a narrow shelf on the medial edge of the shaft. The third trochanter is a large process located more distally on the shaft. The neck of the femur of *Copecion* is longer than that in *Phenacodus*. The fragmentary femur that is known for *Ectocion osbornianus* (UM 91426) is more slender than the femur of *Phenacodus* and it has a narrower and longer patellar trochlea.

Patella.—The patellae of *P. intermedius* (UM 93237), *P. vortmani* (USNM 16691), and *Copecion brachypternus* are similar in shape. The shape of the patella of *Phenacodus trilobatus* differs from that of other phenacodontids in being thicker anteroposteriorly. It has a large area for the insertion of the quadriceps muscle on its proximal extremity.

Tibia.—The overall shape of the tibia of *Copecion* and *Ectocion* (UM 83100) is the same as for other phenacodontids. The medial condyle is larger than the lateral condyle in these and the cranial border is pronounced. The lateral epicondyle forms a strong process for articulation with the astragalus. Well preserved tibiae are known for *Phenacodus intermedius* (UM 93237) and *P. trilobatus* (UM 82241). Overall morphology of the tibia of these taxa is similar, but the tibia of *P. trilobatus* is much more robust (Fig. 58).

Fibula.—No fibula is preserved in either *Copecion* or *Ectocion*, but the morphology of the facets for this bone on the tibia are similar to those of *P. intermedius* (UM 93237) and *P. trilobatus* (UM 65721). The fibula of *Phenacodus* is complete and has a straight shaft with anteroposteriorly elongated proximal and distal joints. The proximal facet is on the proximal extremity of the bone, while the calcaneal facet is oblique on the medial side of the fibula.

Astragalus.—Osborn (1898b) and Radinsky (1966) stated that the astragalar foramen of *Phenacodus intermedius* is absent on the basis of one or more specimens not available to me. Granger (1915) stated in a footnote that
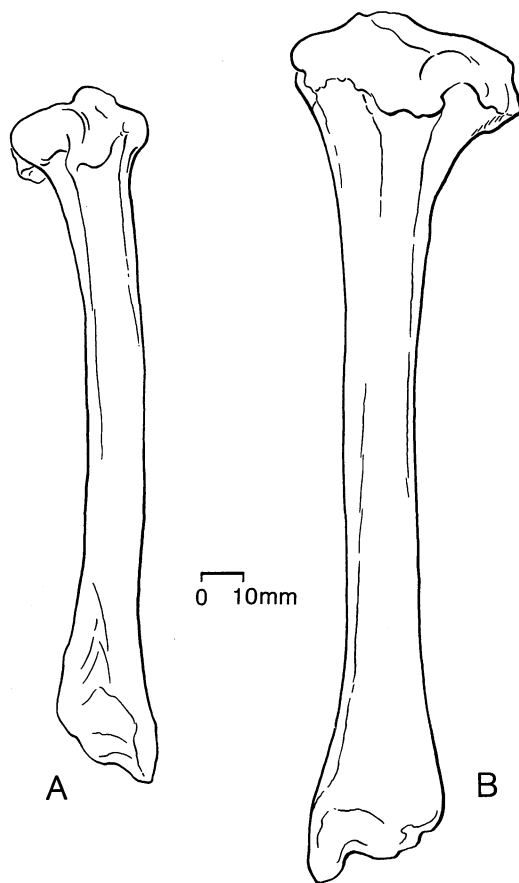
Figure 58. Outlines of right tibia of *Phenacodus intermedius* (A, UM 93237) and left tibia of *P. trilobatus* (B, UM 82241) in anterior view. Notice the difference in robustness.

the foramen is "usually absent in *Phenacodus* but not always" (p. 350). However, the astragalar foramen is small but present in all four *Phenacodus* astragali studied by me. The small size of the foramen causes it to be visible only in well preserved and well prepared specimens (UM 69359, UM 87314, YPM-PU 13208, and YPM-PU 19594). In two of these the astragalar canal can be followed piercing the entire trochlea (UM 87314 and YPM-PU 19594) while the canal is filled with sediment in the other two specimens. The astragalar foramen is present in *Tetraclaenodon* (Matthew, 1897) and absent in *Ectocion* (Radinsky, 1966), *Copecion brachypternus* and *C. davisi* (UM 74077).

The astragalus of *Copecion brachypternus* is similar to those of *Phenacodus grangeri* (YPM-PU 19594), *P. intermedius* (UM 69359), and *P. trilobatus* (UM 87314). The posterior astragalar facet in *Copecion* is directed mediolaterally, whereas it is more proximodistal in *Phenacodus*. The astragali of *Copecion brachypternus* (UM 64179), *C. davisi* (UM 74077), and *Ectocion* (Radinsky, 1966; *E. parvus*, UM 93373) bear a strong ridge on the anterior side of the neck, probably for the attachment of a ligament.

Calcaneus.—The body of the calcaneus of *Phenacodus*, *Copecion*, and *Ectocion* (UM 67243) is distally narrow. The facet for the cuboid is more or less oblique in *Copecion brachypternus* (UM 64179), *C. davisi* (UM 74077), and *Ectocion osbornianus*, whereas it is more perpendicular to the body in *Phenacodus vortmani* (UM 75286), *P. intermedius* (UM 93237) and *P. trilobatus* (UM 68041). The astragalar facet is directed obliquely in *Ectocion* (Radinsky, 1966; UM 93373 and 93384), but more longitudinally in *Copecion* (UM 64179 and 74077) and *Phenacodus*.

Other tarsals.—The navicular and cuboid are known for *Copecion brachypternus*. In morphology they are similar to *Phenacodus trilobatus* (YPM-PU 13208). The calcaneal facet of the cuboid is more oblique in *Copecion*, matching the cuboid facet of the calcaneus. There are no joints between astragalus and cuboid, or between calcaneus and navicular in *Copecion*, *Phenacodus*, or *Tetraclaenodon*.

VII
CONCLUDING REMARKS

Phenacodontids are abundant and diverse in the Paleocene and early Eocene of North America (Table 10, Fig. 59). Four genera are known: *Tetraclaenodon* from the Torrejonian land-mammal age, *Phenacodus* and *Ectocion* from Tiffanian through Bridgerian, and *Copecion* from Clarkforkian and Wasatchian. *Phenacodus* is also known from the Eocene of Europe, but it is always rare at European localities. No definite phenacodontid specimens are known from other continents.

Anatomical knowledge is most complete for *Phenacodus,* which is known from several more or less complete skulls and skeletons. *Copecion* is known only from a partial skeleton, and *Ectocion* from a fragmentary skull and several partial skeletons. *Tetraclaenodon* is known from fragmentary skulls and skeletal fragments.

Dental morphology and function.—Phenacodontids retain the primitive dental formula, and three of the four genera have bunodont teeth. The dental morphology of *Ectocion* is more specialized, it is somewhat lophodont. *Copecion* is characterized by elongate premolars, and *Tetraclaenodon* lacks the mesostyle of the other genera.

Rensberger (1986) studied dental wear in *Tetraclaenodon* and *Phenacodus* and concluded that both taxa used more compressive types of chewing than the primitive condylarth *Protungulatum.* The narrow rostrum and lophodont teeth of *Ectocion* indicate that it may have been more herbivorous than *Phenacodus.* The morphology of the ascending ramus, mode of dental wear, and small sagittal crest are also suggestive of more translative chewing in *Ectocion* (Radinsky, 1966; Rensberger, 1986).

Cranial morphology and function.—The nasal opening of *P. intermedius* is larger than that in *P. vortmani* and *Ectocion.* In addition, the anterior tip of the nasals of *P. intermedius* is retracted. Radinsky (1965) used the position of the tip of the nasals as an indication for the presence of a mobile proboscis in fossil tapiroids, and it is possible that *P. intermedius* also had a short trunk. Its unusually large infraorbital canal is consistent with this, as nervous and vascular supply to upper lip and trunk passes through this canal.

Ectocion is the only phenacodontid for which an ectotympanic auditory bulla is known. An endocranial cast is known only for *Phenacodus.* It has large olfactory bulbs and a small cerebrum and the neencephalon has few fissures (Simpson, 1933).

Postcranial morphology and function.—Osborn (1898b)

and Radinsky (1966) reviewed the postcranial skeleton of *P. intermedius* and their conclusions hold in many respects for all phenacodontids. Phenacodontids have digitigrade and pentadactyl limbs. They are probably cursorial to some extent, but no fusion or reduction of limb elements occurs, except for the absence of the centrale in the carpus. Primitive features of the forelimb include retention of a clavicle (at least in *P. vortmani*) and an unreduced ulna. Cursorial features include the supracondylar foramen of the humerus and the oval shape of the radial head. The hindlimb bears a third trochanter in all phenacodontids, and the fibula is complete. Terminal phalanges are dorsopalmarly flattened, not unlike those of *Hyracotherium.*

Not much is known about the postcranial anatomy of *Ectocion.* The main differences with *Phenacodus* are the weaker deltopectoral crest of the humerus, the weaker greater tubercle of the humerus, and the long and narrow femoral trochlea. These features suggest that the flexors and extensors of shoulder and knee are large in *Ectocion* and indicate that *Ectocion* was more cursorial than *Phenacodus.* Radinsky (1966) noted features of the astragalus and reached a similar conclusion.

Copecion is similar to *Phenacodus* in most aspects of its known postcranial anatomy. Differences include the weaker deltopectoral crest of the humerus, the flat caudal ilium, the longer neck of the femur, and the absence of the astragalar foramen. The direction of the posterior calcaneal facet of the astragalus differs from *Phenacodus,* but is comparable to that of *Ectocion* as described by Radinsky (1966). The weak deltopectoral crest indicates reduced abduction and adduction ability of the shoulder and the absence of the astragalar foramen indicates increased flexion and extension ability of the hindlimb. These features indicate that *Copecion* was also more cursorial than *Phenacodus.*

Sexual dimorphism in Phenacodontidae.—Sexual dimorphism in canine length of *Ectocion osbornianus* was documented in Figure 21. Sexual dimorphism occurs in lower and upper canines, but it is most pronounced in the latter. Presumed female and male dentitions are figured in Figures 18 and 55 respectively. Canine dimorphism for *Phenacodus* cannot be evaluated until larger samples become available.

Sexual dimorphism in *P. intermedius* may also occur in the size of the paranasal sinuses. The paranasal sinuses of one specimen of this taxon are inflated (PU 14864), but

Table 10. Valid phenacodontid taxa and their ranges. Complete names of biochrons are listed in Table 1. Abbreviations in biochron names: Tet., *Tetraclaenodon* zone, *Pant.*, *Pantolambda* zone; *Pl. praec.*, *Plesiadapis praecursor* z.; *Pl. rex*, *Plesiadapis rex* z.; *Pl. chur.*, *Plesiadapis churchilli* z.; *Pl. sim.*, *Plesiadapis simonsi* z.; *Pl. ging.*, *Plesiadapis gingerichi* z.; *Ph. Ec.*, *Phenacodus-Ectocion* z.; *C. tor. Cantius torresi* z.; Lw. *Hap. Ec.*, Lower *Haplomylus-Ectocion* zone; Up. *Hap. Ec.*, Upper *Haplomylus-Ectocion* z.; *Hept.*, *Heptodon* z.; *Lamb.*, *Lambdotherium* z.; *Pal.*, *Palaeosyops* z. Abbreviations of names of land-mammal ages: TO, Torrejonian; TI, Tiffanian; CF, Clarkforkian; WA, Wasatchian; BR, Bridgerian.

Taxon	Zonal range
North America	
Tetraclaenodon puercensis (Cope, 1881)	*Tet.- Pant.* (TO)
T. septentrionalis, new	*Tet.- Pant.* (TO)
Ectocion collinus Russell, 1929	*Pl. praec.-Pl. rex* (TI)
E. cedrus, new	*Pl. rex- Pl. chur.* (TI)
E. mediotuber, new	*Pl. chur.- Pl. sim.* (TI)
E. osbornianus (Cope, 1882a)	*Pl. ging.- Up. Hap. Ec.* (CF-WA)
E. major (Patterson and West, 1973)	*Pl. ging.- Ph. Ect.* (CF)
E. parvus Granger, 1915	*Ph. Ec.- Lw. Hap. Ec.* (CF-WA)
E. superstes Granger, 1915	*Pal.* (BR)
Phenacodus matthewi Simpson, 1935	*Pl. praec.- Pl. sim.* (TI)
P. bisonensis Gazin, 1956	*Pl. praec.-Pl. rex* (TI)
P. grangeri Simpson, 1935	*Pl. rex- Pl. sim.* (TI)
P. magnus, new	*Pl. chur.-Pl. sim.* (TI)
P. vortmani (Cope, 1880)	*Pl. chur.-Pal.* (TI-BR)
P. intermedius Granger, 1915	*Pl. ging.-*BR (TI-BR)
P. trilobatus Cope, 1882	Lw. *Hap. Ec- Lamb.* (WA)
Copecion brachypternus (Cope, 1882)	*Pl. cook.-Hept.* (CF-WA)
C. davisi Gingerich, 1989	*C. torresi* (WA)
Europe	
Phenacodus teilhardi Simpson 1929	Dormaalian
P. lemoinei, new	Dormaalian-Grauvesian
P. condali (Crusafont and Villalta, 1954)	Robiacian

inflation is apparently absent in a specimen exhibited in the American Museum (AMNH 4369; Cope, 1885). Sexual dimorphism in paranasal sinuses could also be present in early perissodactyls. A *Hyracotherium* skull identified as male by Gingerich (1981: AMNH 55266) has inflated paranasal sinuses, whereas these are absent in a female skull (AMNH 55267). If phenacodontids are ancestral to perissodactyls then perissodactyl sexual dimorphism would predate the origin of the order.

Edinger (1950) claimed that paranasal sinuses of mammals have no function, but it is conceivable that they served for sound production, such as the diverticula of the larynx in *Alouatta* (Schoen, 1971) and those between bony and external nares in *Tursiops* (Evans and Maderson, 1973). If the paranasal sinuses of the two sexes differ in size, then they could be important in social behavior. The paranasal sinuses of the only known *Ectocion* skull (UM 86155) are inflated, and the specimen is a presumed male based on canine size. Inflation in *Ectocion* is less pronounced than in *P. intermedius*.

Body weight.—Phenacodontid body weights range over more than an order of magnitude. Their evolution started with forms of medium size, Torrejonian *Tetraclaenodon*. Younger *Ectocion* and *Copecion* radiated into smaller body sizes, the smallest phenacodontids are *E. cedrus, E. parvus*, and *C. davisi*. Most *Phenacodus* are heavier than *Tetraclaenodon*, the largest phenacodontids are *P. magnus* and *P. trilobatus*. Several authors (Alexander et al., 1979; Gingerich et al., 1982; Scott, 1985; Legendre, 1986) have derived allometric equations that can be used to estimate body weights from linear dental and skeletal measures (Table 11). The differences in the resulting estimates mainly reflect differences in the body proportions of phenacodontids and the mammals used to derive the equations. Many of the taxa on which Alexander et al. (1979) and Scott (1985) based their regression coefficients for limb size were more cursorial than phenacodontids, and those derived by Gingerich et al. (1982) were based on primates. Proportions in these taxa are different from those in phenacodontids and the equations may be less useful for estimating phenacodontid body weights. Legendre's (1986) equations based on herbivore tooth size yield probably the most reliable estimates for phenacodontids.

Evolution and ecology.—The genera of phenacodontids

North America   Europe

		North America	Europe
Brid.	Bridgerian undiff.		
	Palaeosyops zone		
Wasatchian	Lambdotherium zone		
	Heptodon zone		
	Bunophorus zone		
	Up. Hapl.-Ect. zone		
	Lw. Hapl.-Ect. zone		
	C. torresi zone		
Clarkf.	Phen. -Ect. zone		
	Pl. cookei zone		
	Pl. gingerichi zone		
Tiffanian	Pl. simonsi zone		
	Pl. churchilli zone		
	Pl. rex zone		
	Pl. anceps zone		
	Pl. praecursor zone		
Torr.	Pantolambda zone	T. puercensis	T. septentrionalis
	Tetraclaenodon zone		

Species ranges shown: E. superstes, E. parvus, E. osbornianus, E. major, E. cedrus, E. mediotuber, E. collinus, C. davisi, C. brachypternus, P. vortmani, P. intermedius, P. matthewi, P. bisonensis, P. grangeri, P. magnus, P. trilobatus, P. teilhardi, P. lemoinei, P. condali

Figure 59. Summary of stratigraphic ranges of species of North American and European Phenacodontidae recognized here.

are easily distinguished on the basis of shape differences in their dentitions. Shape and size differences characterize individual representatives of each of the genera. Differences between taxa are often subtle, and relatively complete specimens are necessary for correct identification. Phenacodontid posterior premolars are typically more diagnostic than molars.

Lineage evolution is apparent in several phenacodontids. It is usually expressed as changes in the proportional representation of different morphologies. Lineage evolution in *Ectocion osbornianus* includes the decreasing frequency of a metaconid on P_3 and an entoconid on P_4. Anagenetic

evolution in characters such as these can only be evaluated on the basis of large samples and is not obvious in poorly known phenacodontids.

Habitat specialization can be documented in Tiffanian and Wasatchian phenacodontids. Tiffanian *Phenacodus* and *Ectocion* occur at localities of different lithologies. The middle and late Tiffanian assemblages are preserved in two classes of sediments, one indicating near-channel, poorly-drained environments and another indicating distal floodplain, well-drained environments. Different phenacodontid taxa occur in contemporaneous assemblages from different sedimentary environments: *Phenacodus magnus*

Table 11. Weight estimates (in kg) of phenacodontids based on measurements on molars and long bones (in mm or mm²). Length and midshaft depth were measured as described by Scott, 1985. Weights were estimated using regression equations on logged data published by Alexander et al. (1979: marked as A) for a broad array of mammals, by Gingerich et al. (1982: G) for primates, by Scott (1985: S) for bovids, and Legendre (1986: L) for herbivores. Estimates from long bones are based on one specimen each, means of a larger sample were used for dental measures.

Taxon, estimator and value used	Weight (kg)	Source
T. puercensis		
M$_1$ (L × W): 51.3 (N = 52)	12.3	G
" "	11.5	L
E. collinus		
M$_1$ (L × W): 33.8 (N = 33)	6.6	G
" "	5.7	L
E. cedrus		
M$_1$ (L × W): 26.5 (N = 68)	4.6	G
" "	3.8	L
E. mediotuber		
M$_1$ (L × W): 32.0 (N = 33)	6.1	G
" "	5.2	L
E. osbornianus		
M$_1$ (L × W): 34.9 (N = 545)	6.9	G
" "	6.0	L
E. major		
M$_1$ (L × W): 66.5 (N = 4)	18.1	G
" "	17.8	L
E. parvus		
M$_1$ (L × W): 23.6 (N = 10)	3.9	G
" "	3.1	L
E. superstes		
M$_1$ (L × W): 55.4 (N = 3)	13.8	G
" "	13.1	L
P. bisonensis		
M$_1$ (L × W): 63.5 (N = 19)	16.9	G
" "	16.5	L
P. grangeri		
M$_1$ (L × W): 112.7 (N = 32)	39.7	G
" "	43.5	L
P. vortmani, Wasatchian		
M$_1$ (L × W): 58.5 (N = 148)	15.0	G
" "	14.3	L
P. magnus		
M$_1$ (L × W): 134.8 (N = 2)	51.9	G
" "	58.8	L
P. intermedius, Wasatchian		
M$_1$ (L × W): 98.3 (N = 35)	32.4	G
" "	34.5	L
Humerus, length: 134	27.0	S
" "	15.0	A
Femur, length: 180	26.0	S
" "	19.0	A
Tibia, length: 155	10.0	A
Tibia, midshaft depth: 18	39.0	A
P. trilobatus		
M$_1$ (L × W): 134.7 (N = 82)	51.8	G
" "	58.7	L
Femur, length: 230	68.0	S
Femur, length: 230	37.0	A
Femur, midshaft depth: 25	77.0	A
Tibia, length: 200	22.0	A
Tibia, midshaft depth: 24	87.0	A
C. brachypternus		
M$_1$ (L × W): 36.7 (N = 84)	7.5	G
" "	6.5	L
Humerus, length: 76	3.3	S
" "	3.0	A
Humerus, midshaft depth: 8.4	4.1	A
Femur, length: 97	2.5	S
" "	3.4	A
Femur, midshaft depth: 7.1	3.4	A
C. davisi		
M$_1$ (L × W): 24.1 (N = 8)	4.0	G
" "	3.2	L

and *Ectocion cedrus* dominate in the poorly-drained environment, while *P. grangeri* and *E. mediotuber* mainly occur in the well-drained environment.

A similar case of habitat specialization may occur in the Wasatchian. Schankler (1981) described the changing pattern of phenacodontid diversity in Bighorn Basin phenacodontids and suggested ecological causes for it. The temporal succession of Bighorn Basin phenacodontids could be the result of differences in preserved sedimentary environment, rather than faunal evolution. Gingerich (1989) suggested a similar explanation for early Wasatchian *Ectocion osbornianus* and *E. parvus*.

Biostratigraphic importance.—Phenacodontids are potentially useful biostratigraphic indicators because of their abundance, but temporal succession of taxa is slow in Clarkforkian through Bridgerian phenacodontids, and phenacodontids are thus of limited biostratigraphic value. The extinction of *Ectocion osbornianus* and restricted range of *E. superstes* are among the few biostratigraphically important events in phenacodontid evolution in the Wasatchian and Bridgerian.

Phenacodontids have real biostratigraphic potential in the Tiffanian, because there is a rapid succession of species in *Phenacodus* and *Ectocion*. Phenacodontid evidence corroborates the tentative age given by Archibald et al. (1987) for the Riverdale locality in the Williston Basin: *P. churchilli* zone. Phenacodontid evidence also suggests revised ages for the White Site and 7-Up Butte in the Powder River Basin and for Seaboard Well in the Bighorn Basin. These localities probably date from the *Plesiadapis churchilli* zone. Phenacodontid fossils corroborate earlier doubts concerning the Clarkforkian age of Buckman Hollow in the Green River Basin (Rose, 1981), suggesting that part of this locality is Tiffanian. The presence of *Ectocion* at UW locality V-77014 (Great Divide Basin) suggests that this locality is Tiffanian and not Torrejonian as thought previously (Winterfeld, 1982). The 23 m level of the Big Bend

National Park section (Schiebout, 1974) is here considered *Plesiadapis rex* zone on the basis of phenacodontid evidence, and not *P. praecursor* zone as stated by Archibald et al. (1987).

Intercontinental correlation.—Representatives of the genus *Phenacodus* are known from North America and Europe and can be evaluated in the light of recent ideas concerning the correlation of European and North American Eocene faunas (e.g., Rose, 1981; Gingerich, 1989). Three taxa of European *Phenacodus* are known from the Eocene of Europe. These taxa are very incompletely known, but consecutive stages show an increase in the size of phenacodontids. Morphological similarities suggesting that the European taxa are closely related include a short dentary, with few diastemata and a fused mandibular symphysis.

The earliest European *Phenacodus* resembles *P. vortmani* in size. *P. vortmani* is known from Tiffanian through Bridgerian land-mammal ages, and North American occurrences thus predate European occurrences. The main faunal exchange between North America and Europe took place near the base of the Dormaalian (Godinot, 1981), and it is thus likely that this faunal exchange included North American *Phenacodus vortmani* migrating to Europe.

Most *Phenacodus vortmani* lacks the fused mandibular symphysis and short dentary of European *Phenacodus,* but a specimen tentatively referred to *P. vortmani* (UM 83622) from the *Cantius torresi* zone of the Clarks Fork Basin lacks diastemata and does resemble European *Phenacodus* in these respects.

The importance of this resemblance remains unclear until more material becomes available, but it could corroborate Gingerich's (1989) hypothesis that the *Cantius torresi* zone of the Western Interior correlates with and even predates slightly the Dormaalian of Europe.

Phylogeny.—The present study mainly investigated phenacodontid morphology and evolution at the lowest taxonomic level. As such, it is a necessary precursor to broader scale studies concerning evolutionary problems in which phenacodontids play a role.

One of the most interesting remaining problems is the possible relation between phenacodontids and perissodactyls. Traditionally phenacodontids were held to be ancestral to perissodactyls (Radinsky, 1966; Carroll, 1988). Fischer (1986, 1990) and Prothero et al. (1988) have challenged this opinion and claimed that Hyracoidea were the sister group of phenacodontids. These two views are only consistent if phenacodontids are ancestral to both hyracoids and perissodactyls, but other authors dispute perissodactyl-hyracoid relationships (e.g., Novacek and Wyss, 1986; Novacek et al., 1988; Tassy and Shoshani, 1988). As pointed out by Fischer (1986), phenacodontids play a key role in resolving this controversy.

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APPENDIX I

Appendix I. Summary statistics for some phenacodontid samples (in mm). Listed are respectively: number of specimens (N), minimum (Min), maximum (Max), mean, standard deviation (SD), and coefficient of variation (V).

Table A-1. Summary statistics for *Tetraclaenodon puercensis*, *Pantolambda* zone, Rock Bench Quarry.

	N	Min	Max	Mean	SD	V
P_3, length	13	6.4	8.4	7.45	0.62	8.3
P_3, width	12	3.7	5.4	4.42	0.58	12.2
P_4, length	16	6.9	8.5	7.69	0.40	5.2
P_4, width	15	4.7	6.1	5.34	0.34	6.3
M_1, length	16	7.0	8.2	7.81	0.31	3.9
M_1, width trigonid	17	5.8	7.0	6.38	0.33	5.0
M_2, length	15	7.2	8.3	7.90	0.40	5.0
M_2, width trigonid	16	6.2	7.5	6.79	0.44	6.4
M_3, length	9	6.9	9.0	8.08	0.62	7.6
M_3, width trigonid	7	5.3	6.2	5.74	0.31	5.3
P^3, length	2	6.8	7.2	7.00	0.29	4.1
P^3, width	2	5.9	6.6	6.25	0.50	7.9
P^4, length	13	6.1	8.0	6.97	0.47	6.6
P^4, width	13	6.7	8.7	7.87	0.61	7.7
M^1, length	7	7.2	8.2	7.69	0.31	4.1
M^1, width	7	8.8	10.1	9.64	0.45	4.7
M^2, length	9	7.5	8.5	8.06	0.34	4.2
M^2, width	9	9.3	10.8	9.90	0.52	5.2
M^3, length	21	6.1	8.1	7.12	0.56	7.9
M^3, width	20	6.7	7.9	7.19	0.33	4.5

Table A-2. Summary statistics for *Tetraclaenodon puercensis*, *Tetraclaenodon* zone, Big Pocket.

	N	Min	Max	Mean	SD	V
P_3, length	6	6.5	8.0	7.03	0.57	8.0
P_3, width	7	3.5	4.7	4.28	0.39	9.1
P_4, length	14	6.8	8.4	7.39	0.44	6.0
P_4, width	14	4.6	5.5	5.12	0.29	5.6
M_1, length	17	7.0	8.7	7.68	0.41	5.3
M_1, width trigonid	18	5.5	7.5	6.36	0.53	8.3
M_2, length	27	7.1	9.0	7.76	0.50	6.4
M_2, width trigonid	27	6.4	7.7	6.93	0.39	5.7
M_3, length	23	6.9	9.9	7.93	0.72	9.0
M_3, width trigonid	27	5.3	7.0	5.81	0.43	7.4
P^3, length	3	6.2	7.5	7.07	0.76	10.6
P^3, width	3	5.4	6.5	6.13	0.64	10.4
P^4, length	6	6.4	8.2	7.27	0.58	7.9
P^4, width	5	6.4	9.4	7.88	1.15	14.5
M^1, length	9	7.3	8.5	7.88	0.42	5.3
M^1, width	9	8.6	10.3	9.38	0.64	6.7
M^2, length	9	7.3	9.1	8.27	0.51	6.1
M^2, width	9	7.6	11.1	9.60	1.05	10.9
M^3, length	10	6.2	8.1	7.02	0.65	9.2
M^3, width	9	5.8	8.0	6.91	0.79	11.4

Table A-3. Summary statistics for *Tetraclaenodon septentrionalis*, *Pantolambda* zone, Crazy Mountain Basin.

	N	Min	Max	Mean	SD	V
P^3, length	1			8.3		
P^3, width	1			7.3		
M^1, length	1			8.3		
M^1, width	1			10.3		
M^2, length	2	9.5	10.3	9.90	0.57	5.8
M^2, width	2	10.7	12.4	11.55	1.20	10.4
M^3, length	1			8.0		
M^3, width	1			7.9		
M^3, width	20	6.7	7.9	7.19	0.33	4.5

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Table A-4. Summary statistics for *Ectocion collinus*, *Plesiadapis praecursor* zone, Douglass Quarry.

	N	Min	Max	Mean	SD	V
P_3, length	9	5.2	6.0	5.51	0.27	4.9
P_3, width	9	2.8	3.6	3.29	0.29	8.8
P_4, length	16	5.4	7.3	6.54	0.43	6.6
P_4, width	16	4.1	4.7	4.44	0.17	3.8
M_1, length	20	6.1	7.4	6.59	0.39	5.9
M_1, width trigonid	17	4.6	5.6	5.19	0.28	5.4
M_2, length	21	6.2	7.4	6.71	0.31	4.6
M_2, width trigonid	20	5.0	5.9	5.59	0.22	3.9
M_3, length	32	6.2	8.4	7.34	0.53	7.2
M_3, width trigonid	32	3.8	5.4	4.81	0.34	7.1
P^3, length	10	5.3	6.2	5.60	0.32	5.6
P^3, width	11	4.5	5.7	5.05	0.39	7.6
P^4, length	15	5.3	6.5	5.83	0.32	5.5
P^4, width	17	5.5	7.7	6.76	0.54	8.0
M^1, length	8	6.8	7.7	7.21	0.27	3.7
M^1, width	8	7.9	8.8	8.39	0.36	4.2
M^2, length	5	6.9	8.0	7.40	0.41	5.5
M^2, width	5	7.9	8.8	8.36	0.39	5.0
M^3, length	26	5.5	7.3	6.39	0.50	7.7
M^3, width	23	6.2	8.4	7.07	0.64	9.0

Table A-6. Summary statistics for *Ectocion mediotuber*, *Plesiadapis simonsi* zone, Clarks Fork Basin.

	N	Min	Max	Mean	SD	V
P_3, length	7	5.1	6.1	5.70	0.36	6.2
P_3, width	7	3.3	3.7	3.51	0.15	4.1
P_4, length	17	5.4	7.1	6.26	0.49	7.7
P_4, width	20	3.9	5.1	4.37	0.37	8.3
M_1, length	33	5.6	7.2	6.38	0.40	6.2
M_1, width trigonid	32	4.4	5.5	5.06	0.31	6.1
M_2, length	27	6.0	7.2	6.57	0.30	4.6
M_2, width trigonid	32	4.9	6.0	5.38	0.30	5.4
M_3, length	21	6.1	7.9	7.22	0.50	6.9
M_3, width trigonid	20	3.7	5.0	4.58	0.40	8.7
P^3, length	3	5.4	6.3	5.77	0.48	8.2
P^3, width	5	5.3	6.1	5.50	0.34	6.2
P^4, length	8	4.7	6.6	5.91	0.60	10.2
P^4, width	11	6.4	8.1	7.06	0.47	6.6
M^1, length	17	5.6	8.0	6.94	0.56	8.1
M^1, width	18	7.4	9.1	8.18	0.60	7.0
M^2, length	18	6.4	8.9	7.46	0.61	8.2
M^2, width	25	7.2	9.5	8.28	0.62	7.5
M^3, length	19	5.3	7.5	6.32	0.61	9.7
M^3, width	17	5.8	8.3	6.74	0.66	9.8

Table A-5. Summary statistics for *Ectocion cedrus*, *Plesiadapis rex* zone, Cedar Point Quarry.

	N	Min	Max	Mean	SD	V
P_3, length	21	4.4	5.6	4.96	0.39	7.8
P_3, width	22	2.4	3.7	3.02	0.33	10.9
P_4, length	28	5.2	6.5	5.94	0.34	5.7
P_4, width	28	3.2	4.4	3.96	0.26	6.6
M_1, length	56	5.3	7.0	6.00	0.33	5.5
M_1, width trigonid	57	4.0	5.0	4.45	0.25	5.5
M_2, length	70	5.5	7.3	6.36	0.34	5.3
M_2, width trigonid	71	4.4	5.7	4.95	0.28	5.7
M_3, length	46	6.0	8.1	6.90	0.43	6.2
M_3, width trigonid	44	3.5	5.1	4.31	0.33	7.4
P^3, length	4	5.1	6.0	5.43	0.41	7.4
P^3, width	4	4.8	5.7	5.23	0.37	7.0
P^4, length	7	5.1	6.1	5.80	0.36	6.3
P^4, width	7	6.2	7.5	6.77	0.46	6.8
M^1, length	10	6.3	7.4	6.72	0.40	5.9
M^1, width	10	7.1	8.6	7.78	0.48	6.1
M^2, length	8	6.5	8.0	7.30	0.55	7.5
M^2, width	7	7.2	9.2	8.16	0.60	7.3
M^3, length	13	5.4	7.9	6.28	0.67	10.8
M^3, width	13	5.9	8.1	6.76	0.57	8.4

Table A-7. Summary statistics for *Ectocion osbornianus*, *Plesiadapis gingerichi* zone, Bighorn Basin.

	N	Min	Max	Mean	SD	V
P_3, length	10	6.0	7.7	6.99	0.54	7.8
P_3, width	11	3.5	4.7	4.03	0.36	8.9
P_4, length	18	6.0	7.8	7.14	0.42	8.6
P_4, width	20	4.3	5.8	4.96	0.34	6.9
M_1, length	24	6.0	7.7	6.78	0.43	6.3
M_1, width trigonid	24	4.9	6.2	5.57	0.35	6.3
M_2, length	34	6.0	7.6	6.92	0.41	5.9
M_2, width trigonid	35	5.0	6.7	5.84	0.43	7.4
M_3, length	19	6.3	8.3	7.44	0.53	7.1
M_3, width trigonid	20	4.2	5.8	4.93	0.40	8.0
P^4, length	9	5.8	7.4	6.54	0.52	7.9
P^4, width	11	7.4	8.6	7.95	0.40	5.0
M^1, length	13	6.8	8.0	7.36	0.42	5.7
M^1, width	14	7.3	9.4	8.61	0.64	7.4
M^2, length	17	6.9	8.7	7.77	0.48	6.2
M^2, width	16	8.0	10.1	9.02	0.61	6.7
M^3, length	11	5.8	7.8	6.44	0.57	8.8
M^3, width	11	6.8	8.0	7.19	0.34	4.6

Table A-8. Summary statistics for *Ectocion osbornianus*, *Plesiadapis cookei* zone, Bighorn Basin.

	N	Min	Max	Mean	SD	V
P_3, length	49	5.7	7.3	6.60	0.36	5.3
P_3, width	52	3.0	4.3	3.70	0.28	7.4
P_4, length	98	5.8	7.7	6.70	0.37	5.4
P_4, width	103	4.1	5.8	4.70	0.30	6.3
M_1, length	173	5.8	7.5	6.56	0.34	5.1
M_1, width trigonid	181	4.5	6.4	5.22	0.31	6.0
M_2, length	178	5.6	7.6	6.70	0.36	5.3
M_2, width trigonid	187	4.5	6.6	5.56	0.35	6.3
M_3, length	91	6.3	8.2	7.21	0.44	6.1
M_3, width trigonid	105	4.1	6.1	4.77	0.34	7.2
P^3, length	45	5.2	6.7	6.15	0.34	5.5
P^3, width	46	4.9	6.9	6.16	0.50	8.0
P^4, length	53	5.8	7.2	6.61	0.37	5.5
P^4, width	54	5.6	8.8	7.78	0.57	7.3
M^1, length	85	6.4	8.0	7.23	0.40	5.4
M^1, width	88	7.3	10.0	8.74	0.45	5.1
M^2, length	96	6.2	8.9	7.58	0.53	7.0
M^2, width	108	7.7	10.1	8.88	0.47	5.3
M^3, length	63	5.2	7.5	6.23	0.46	7.4
M^3, width	66	5.6	8.0	7.00	0.47	6.7

Table A-9. Summary statistics for *Ectocion osbornianus*, *Phenacodus-Ectocion* zone, Bighorn Basin.

	N	Min	Max	Mean	SD	V
P_3, length	21	6.0	7.8	6.62	0.49	7.3
P_3, width	25	3.4	4.6	3.93	0.29	7.3
P_4, length	64	5.7	7.8	6.67	0.37	5.5
P_4, width	65	3.9	5.8	4.73	0.29	6.1
M_1, length	88	5.6	7.6	6.55	0.37	5.7
M_1, width trigonid	90	4.2	6.1	5.23	0.34	6.4
M_2, length	79	5.9	7.5	6.72	0.34	3.0
M_2, width trigonid	78	4.7	6.4	5.63	0.39	6.9
M_3, length	36	6.0	8.1	7.19	0.39	5.5
M_3, width trigonid	44	4.1	5.7	4.76	0.37	7.6
P^3, length	14	5.5	7.8	6.29	0.56	9.0
P^3, width	17	5.6	7.0	6.28	0.44	7.0
P^4, length	26	6.0	7.6	6.72	0.46	6.8
P^4, width	31	7.1	9.4	8.05	0.58	7.2
M^1, length	36	6.4	8.0	7.36	0.37	5.0
M^1, width	41	7.9	9.8	8.87	0.43	4.8
M^2, length	45	6.7	8.7	7.66	0.59	7.6
M^2, width	48	7.1	10.0	8.86	0.60	6.6
M^3, length	31	4.5	8.0	6.36	0.59	9.3
M^3, width	32	6.1	9.0	7.33	0.62	8.4

Table A-10. Summary statistics for *Ectocion osbornianus*, Lower *Haplomylus-Ectocion* zone, Bighorn Basin.

	N	Min	Max	Mean	SD	V
P_3, length	75	5.8	8.2	6.90	0.48	6.9
P_3, width	83	3.1	4.3	3.82	0.26	6.6
P_4, length	163	5.9	8.1	6.88	0.45	6.4
P_4, width	172	4.1	5.5	4.77	0.30	6.1
M_1, length	233	5.5	8.2	6.63	0.38	5.8
M_1, width trigonid	233	4.4	6.3	5.32	0.33	6.2
M_2, length	234	5.8	8.0	6.83	0.39	5.6
M_2, width trigonid	240	4.8	6.6	5.70	0.33	5.6
M_3, length	117	6.1	8.2	7.15	0.38	5.2
M_3, width trigonid	135	4.1	5.8	4.81	0.31	6.3
P^3, length	33	5.5	7.2	6.39	0.41	6.4
P^3, width	35	5.4	7.2	6.20	0.45	7.1
P^4, length	54	5.7	7.7	6.56	0.40	6.0
P^4, width	59	6.5	8.9	7.68	0.46	5.9
M^1, length	98	6.3	8.1	7.23	0.39	5.3
M^1, width	109	7.6	9.9	8.73	0.49	5.5
M^2, length	109	6.6	8.3	7.48	0.42	5.5
M^2, width	115	7.6	10.9	8.83	0.48	5.3
M^3, length	72	5.4	7.9	6.36	0.51	7.9
M^3, width	68	6.1	8.6	7.10	0.51	7.0

Table A-11. Summary of statistics for *Ectocion osbornianus*, Upper *Haplomylus-Ectocion* zone, Bighorn Basin.

	N	Min	Max	Mean	SD	V
P_3, length	13	5.9	7.8	6.91	0.48	6.9
P_3, width	13	3.8	4.6	4.16	0.25	5.9
P_4, length	22	6.5	7.6	7.15	0.36	5.0
P_4, width	23	4.6	5.5	5.02	0.26	5.2
M_1, length	23	5.9	7.5	6.90	0.39	5.6
M_1, width trigonid	21	5.2	6.3	5.63	0.28	5.0
M_2, length	30	6.0	8.3	7.00	0.50	7.0
M_2, width trigonid	31	5.2	6.8	5.81	0.39	6.6
M_3, length	20	6.4	8.0	7.32	0.42	5.8
M_3, width trigonid	23	4.4	5.4	4.93	0.30	6.1
P^3, length	5	6.0	6.7	6.48	0.28	4.3
P^3, width	5	5.8	7.4	6.74	0.67	9.9
P^4, length	4	6.2	7.1	6.67	0.41	6.0
P^4, width	4	7.3	8.8	8.03	0.74	9.2
M^1, length	13	6.9	8.5	7.68	0.52	6.6
M^1, width	11	8.4	9.8	8.86	0.41	4.5
M^2, length	12	6.6	8.6	7.64	0.61	8.0
M^2, width	9	8.2	9.2	8.84	0.37	4.1
M^3, length	8	6.3	7.2	6.75	0.31	4.5
M^3, width	8	7.3	8.1	7.75	0.26	3.3

Table A-12. Summary statistics of *Ectocion major*, Clarkforkian, Piceance Basin.

	N	Min	Max	Mean	SD	V
P_3, length	2	7.5	7.5	7.50		
P_3, width	3	4.5	4.5	4.50		
P_4, length	2	8.1	8.3	8.20	0.15	1.7
P_4, width	2	5.7	6.0	5.85	0.22	3.6
M_1, length	3	8.6	9.1	8.90	0.27	2.9
M_1, width trigonid	3	6.5	7.8	7.27	0.69	9.4
M_2, length	3	8.8	9.4	9.17	0.32	3.5
M_2, width trigonid	3	7.3	7.8	7.50	0.27	3.5
M_3, length	3	9.1	10.2	9.70	0.56	5.7
M_3, width trigonid	3	6.3	6.8	6.50	0.27	4.1

Table A-13. Summary statistics for *Ectocion parvus*, *Cantius torresi* zone, Bighorn Basin.

	N	Min	Max	Mean	SD	V
P_3, length	3	5.5	6.0	5.77	0.26	4.4
P_3, width	4	2.8	3.2	3.05	0.18	5.6
P_4, length	14	5.1	6.3	5.78	0.33	5.8
P_4, width	14	3.4	4.2	3.77	0.23	6.0
M_1, length	11	5.2	5.9	5.47	0.22	4.0
M_1, width trigonid	9	3.8	4.8	4.36	0.29	6.7
M_2, length	10	4.6	5.9	5.48	0.38	6.9
M_2, width trigonid	14	4.2	5.2	4.64	0.25	5.2
M_3, length	6	5.1	6.2	5.88	0.42	7.1
M_3, width trigonid	8	3.4	4.3	3.83	0.33	8.7
P^3, length	2	5.0	5.4	5.20	0.29	5.4
P^3, width	2	5.0	5.3	5.15	0.22	4.1
P^4, length	2	5.5	5.7	5.60	0.15	2.5
P^4, width	2	6.3	6.8	6.55	0.36	5.4
M^1, length	4	5.6	6.2	5.67	0.06	1.0
M^1, width	4	7.3	7.4	7.37	0.06	.8
M^2, length	8	5.7	7.0	6.33	0.38	5.9
M^2, width	7	6.7	7.8	7.30	0.45	6.1
M^3, length	5	4.4	5.8	5.20	0.67	12.7
M^3, width	5	5.5	6.6	6.06	0.49	8.0

Table A-14. Summary statistics for *Ectocion superstes*, *Palaeosyops* zone, Wind River Basin.

	N	Min	Max	Mean	SD	V
P_3, length	2	7.0	8.6	7.80	1.13	14.4
P_3, width	2	3.7	4.2	4.95	0.36	9.0
P_4, length	3	7.9	8.2	8.00	0.18	2.2
P_4, width	3	5.4	5.7	5.57	0.16	2.8
M_1, length	3	7.7	8.6	8.20	0.46	5.6
M_1, width trigonid	3	6.5	6.9	6.77	0.23	3.4
M_2, length	2	7.9	8.2	8.05	0.22	2.6
M_2, width trigonid	3	6.7	7.2	6.97	0.26	3.6
M_3, length	2	8.8	10.8	9.80	1.42	14.4
M_3, width trigonid	2	6.1	8.1	7.10	1.42	19.8
P^4, length	1			7.0		
P^4, width	1			8.4		
M^1, length	2	7.6	8.1	7.85	0.36	4.5
M^1, width	2	9.9	10.3	10.10	0.29	2.8
M^2, length	1			8.3		
M^2, width	1			10.2		
M^3, length	3	7.1	9.8	8.10	1.48	12.4
M^3, width	3	8.2	9.5	8.73	0.69	7.8

Table A-15. Summary statistics for *Phenacodus bisonensis*, *Plesiadapis praecursor* zone, Douglass Quarry.

	N	Min	Max	Mean	SD	V
P_3, width	1			3.6		
P_4, length	7	9.0	10.3	9.56	0.48	5.0
P_4, width	7	5.7	6.8	6.24	0.40	6.4
M_1, length	2	9.5	9.7	9.60	0.15	1.5
M_1, width trigonid	2	7.0	7.7	7.35	0.50	6.7
M_2, length	2	9.6	10.0	9.80	0.29	2.9
M_2, width trigonid	2	7.9	8.3	8.10	0.28	3.5
M_3, length	5	9.4	10.6	10.22	0.50	4.9
M_3, width trigonid	7	6.5	7.4	6.97	0.34	4.8
P^3, width	1			7.1		
P^4, length	5	8.3	9.2	8.78	0.38	4.4
P^4, width	4	9.1	9.7	9.43	0.28	2.9

Table A-16. Summary statistics for *Phenacodus bisonensis*, *Plesiadapis anceps* zone, Bison Basin.

	N	Min	Max	Mean	SD	V
P_3, length	3	7.7	9.0	8.33	0.65	7.8
P_3, width	3	4.8	5.6	5.30	0.44	8.2
P_4, length	6	7.7	9.2	8.76	0.58	6.6
P_4, width	7	5.7	6.6	6.01	0.34	5.7
M_1, length	8	8.5	9.4	8.89	0.34	3.9
M_1, width trigonid	8	6.3	7.4	7.01	0.38	5.4
M_2, length	9	8.5	9.7	8.92	0.36	4.0
M_2, width trigonid	8	6.9	7.8	7.43	0.32	4.3
M_3, length	6	9.1	11.0	9.6	0.72	7.5
M_3, width trigonid	6	5.9	7.2	6.50	0.51	7.8
P^3, length	1			7.5		
P^3, width	1			8.9		
P^4, length	2	8.1	8.4	8.25	0.21	2.7
P^4, width	2	9.2	9.4	9.30	0.15	1.5
M^2, length	5	9.4	11.0	10.10	0.71	7.0
M^2, width	6	10.3	11.3	10.77	0.41	3.9
M^3, length	7	7.9	9.2	8.58	0.52	6.0
M^3, width	7	8.1	9.7	8.74	0.56	6.5

Table A-17. Summary statistics for *Phenacodus bisonensis*, *Plesiadapis rex* zone, Bison Basin.

	N	Min	Max	Mean	SD	V
P_4, length	3	8.6	9.4	8.93	0.42	4.7
P_4, width	3	5.5	6.3	5.93	0.41	6.8
M_1, length	5	8.7	9.1	8.82	0.18	2.0
M_1, width trigonid	6	6.6	7.5	7.15	0.33	4.6
M_2, length	4	9.2	9.8	9.40	0.29	3.0
M_2, width trigonid	4	7.3	8.2	7.85	0.41	5.1
M_3, length	3	10.2	10.8	10.43	0.33	3.1
M_3, width trigonid	3	7.0	7.7	7.27	0.38	5.2
P^3, length	1			7.9		
P^3, width	1			6.5		
P^4, length	3	7.2	8.4	7.87	0.62	7.8
P^4, width	3	7.9	9.1	8.33	0.67	8.0
M^1, length	2	9.4	9.9	9.65	0.36	3.7
M^1, width	3	9.7	11.2	10.67	0.84	7.8
M^2, length	3	9.2	10.8	10.23	0.90	8.8
M^2, width	3	9.9	11.9	11.13	1.08	9.7
M^3, length	1			9.6		
M^3, width	1			9.6		

Table A-18. Summary statistics for *Phenacodus grangeri*, *Plesiadapis rex* zone, Cedar Point Quarry.

	N	Min	Max	Mean	SD	V
P_3, length	3	8.9	9.4	9.10	0.27	2.9
P_3, width	3	4.7	6.3	5.40	0.82	15.1
P_4, length	7	9.8	11.1	10.54	0.40	3.8
P_4, width	7	7.0	8.2	7.54	0.47	5.9
M_1, length	9	10.5	11.6	11.00	0.39	3.5
M_1, width trigonid	8	8.4	10.1	9.00	0.68	7.5
M_2, length	12	9.8	12.2	10.82	0.68	6.3
M_2, width trigonid	13	8.6	11.2	9.59	0.84	9.7
M_3, length	13	10.5	12.8	11.90	0.77	6.4
M_3, width trigonid	12	7.1	10.1	8.50	0.79	9.2
P^3, length	8	9.1	10.4	9.73	0.49	5.0
P^3, width	10	8.5	10.4	9.67	0.62	6.4
P^4, length	12	8.5	10.4	9.49	0.58	6.1
P^4, width	12	10.0	11.8	11.00	0.62	5.6
M^1, length	24	10.0	13.1	11.48	0.82	7.2
M^1, width	21	12.1	15.1	13.27	0.79	5.6
M^2, length	22	10.8	13.3	12.15	0.78	6.4
M^2, width	22	12.3	15.3	13.86	0.76	5.4
M^3, length	20	9.2	12.3	10.85	0.65	6.0
M^3, width	20	9.4	12.8	10.99	0.84	7.6

Table A-19. *Phenacodus grangeri*, *Plesiadapis simonsi* zone, Bighorn Basin.

	N	Min	Max	Mean	SD	V
P_3, length	8	9.2	10.3	9.94	0.36	3.5
P_3, width	9	5.9	6.9	6.32	0.36	5.5
P_4, length	14	9.9	11.9	11.15	0.97	8.7
P_4, width	12	7.1	8.4	7.96	0.40	5.0
M_1, length	14	10.2	13.0	11.81	0.78	6.6
M_1, width trigonid	15	9.1	10.8	10.0	0.38	3.8
M_2, length	19	11.1	12.9	11.85	0.44	3.7
M_2, width trigonid	18	9.8	11.7	10.72	0.49	4.5
M_3, length	26	10.4	14.2	12.52	0.87	7.0
M_3, width trigonid	26	7.5	10.6	8.89	0.60	6.7
P^3, length	7	9.0	10.0	9.60	0.33	3.3
P^3, width	6	8.2	9.4	8.77	0.59	6.7
P^4, length	12	8.7	10.1	9.43	0.52	5.5
P^4, width	11	10.4	11.7	11.04	0.48	4.3
M^1, length	6	10.5	11.7	11.13	0.48	4.2
M^1, width	5	12.1	13.5	12.78	0.56	4.4
M^2, length	15	10.0	12.8	11.80	0.85	7.1
M^2, width	17	12.0	14.3	13.11	0.66	5.0
M^3, length	17	9.2	12.3	10.72	0.82	7.6
M^3, width	18	9.1	12.1	10.21	0.85	8.3

Table A-20. Summary statistics for *Phenacodus magnus*, *Plesiadapis simonsi* zone, Clarks Fork Basin.

	N	Min	Max	Mean	SD	V
P_4, length	2	12.3	14.3	13.30	1.41	10.6
P_4, width	2	8.9	9.9	9.40	0.71	7.5
M_1, length	1			14.2		
M_1, width trigonid	1			11.4		
M_2, length	1			14.5		
M_2, width trigonid	1			12.6		
P^3, width	1			10.0		
P^4, length	4	10.6	12.6	11.63	1.13	9.7
P^4, width	4	12.1	13.6	13.00	0.70	5.4
M^1, length	5	12.1	14.1	13.20	0.73	5.5
M^1, width	4	14.2	15.5	14.95	0.58	3.9
M^2, length	5	13.3	14.3	14.10	0.45	3.2
M^2, width	5	15.1	15.7	15.42	0.28	1.8
M^3, length	2	11.0	12.3	11.65	0.92	7.9
M^3, width	3	10.2	13.3	11.57	1.58	13.7

Table A-21. Summary statistics for *Phenacodus vortmani*, *Plesiadapis simonsi* zone

	N	Min	Max	Mean	SD	V
P_3, length	3	8.1	8.8	8.47	0.36	4.1
P_3, width	3	5.4	5.7	5.60	0.18	3.1
P_4, length	6	9.1	9.8	9.48	0.25	2.6
P_4, width	6	5.7	7.1	6.48	0.52	8.0
M_1, length	4	9.0	10.0	9.63	0.45	4.7
M_1, width trigonid	3	7.2	7.9	7.67	0.41	5.3
M_2, length	5	9.5	10.0	9.66	0.21	2.1
M_2, width trigonid	7	7.7	8.4	8.10	0.28	3.4
M_3, length	7	8.5	11.0	9.84	0.81	8.2
M_3, width trigonid	7	6.3	7.6	6.91	0.56	8.0
P^4, width	1			9.6		
M^1, length	2	9.0	9.8	9.40	0.57	6.0
M^1, width	2	10.9	11.4	11.15	0.35	3.2
M^2, length	2	9.5	10.0	9.75	0.35	3.6
M^2, width	2	10.4	10.6	10.50	0.14	1.3
M^3, length	4	8.6	10.3	9.48	0.70	7.3
M^3, width	4	7.7	9.6	8.88	0.83	9.3

Table A-22. Summary statistics for *Phenacodus vortmani*, *Phenacodus-Ectocion* zone, Clarks Fork Basin.

	N	Min	Max	Mean	SD	V
P_3, length	2	8.7	9.2	8.95	0.36	4.0
P_3, width	1			5.2		
P_4, length	7	9.0	10.2	9.71	0.50	4.7
P_4, width	8	5.8	6.7	6.10	0.31	5.1
M_1, length	6	8.5	10.1	9.32	0.59	6.2
M_1, width trigonid	7	7.3	8.1	7.66	0.37	4.8
M_2, length	8	8.1	9.6	9.09	0.47	5.1
M_2, width trigonid	9	7.3	8.8	7.79	0.47	5.9
M_3, length	10	9.0	10.3	9.53	0.41	4.2
M_3, width trigonid	10	5.9	7.5	6.78	0.44	6.4
P^3, length	2	7.8	9.5	8.65	1.21	13.9
P^3, width	2	6.7	7.4	7.05	0.50	7.0
P^4, length	1			8.5		
P^4, width	2	8.9	9.7	9.30	0.57	6.1
M^1, length	4	8.7	9.8	9.35	0.48	5.1
M^1, width	3	10.0	11.0	10.57	0.51	4.8
M^2, length	4	9.3	10.4	10.08	0.52	5.2
M^2, width	5	9.7	11.1	10.56	0.53	5.0
M^3, length	2	8.1	9.0	8.55	0.64	7.4
M^3, width	3	8.1	8.5	8.33	0.21	2.5

Table A-23. Summary statistics for *Phenacodus vortmani*, Lower *Haplomylus-Ectocion* zone, Bighorn Basin.

	N	Min	Max	Mean	SD	V
P_3, length	10	7.1	9.1	7.97	0.62	7.8
P_3, width	11	4.1	5.4	4.70	0.43	9.1
P_4, length	23	7.9	10.3	8.88	0.72	8.2
P_4, width	27	5.1	7.2	5.95	0.60	9.9
M_1, length	30	7.4	10.0	8.51	0.65	7.5
M_1, width trigonid	32	6.1	8.6	7.04	0.55	7.7
M_2, length	27	7.6	10.7	8.53	0.73	8.5
M_2, width trigonid	26	6.1	9.1	7.33	0.68	9.2
M_3, length	18	7.4	10.2	8.44	0.68	8.0
M_3, width trigonid	19	5.3	8.2	6.16	0.77	12.5
P^3, length	1			8.2		
P^3, width	2	7.3	7.8	7.55	0.36	4.7
P^4, length	4	7.3	8.3	7.63	0.48	6.2
P^4, width	3	8.3	8.5	8.43	0.12	1.4
M^1, length	10	8.3	10.3	8.73	0.60	6.8
M^1, width	10	9.5	10.9	10.02	0.50	4.9
M^2, length	7	8.3	11.0	8.99	1.06	11.7
M^2, width	8	9.3	10.8	9.80	0.58	5.8
M^3, length	6	7.0	10.3	8.05	1.20	14.8
M^3, width	6	6.6	8.9	7.48	0.93	12.4

Table A-24. Summary statistics for *Phenacodus vortmani*, *Bunophorus* zone, Bighorn Basin.

	N	Min	Max	Mean	SD	V
P_3, length	17	7.2	9.2	7.92	0.50	6.3
P_3, width	18	4.0	5.1	4.67	0.27	5.6
P_4, length	32	8.1	10.0	8.75	0.47	5.3
P_4, width	33	5.3	6.5	5.97	0.31	5.1
M_1, length	32	7.4	8.9	8.28	0.31	3.7
M_1, width trigonid	31	6.1	7.8	7.00	0.34	4.7
M_2, length	24	7.8	9.5	8.40	0.40	4.8
M_2, width trigonid	25	5.6	7.8	7.18	0.44	6.0
M_3, length	26	8.0	9.5	8.82	0.43	4.8
M_3, width trigonid	24	5.8	6.7	6.25	0.27	4.2
P^3, length	5	6.8	7.5	7.22	0.30	4.1
P^3, width	6	6.8	7.7	7.10	0.37	5.2
P^4, length	17	7.2	9.4	7.88	0.57	7.2
P^4, width	18	7.1	10.7	8.86	0.73	8.1
M^1, length	18	8.0	9.3	8.51	0.42	4.8
M^1, width	16	9.7	11.1	10.30	0.40	3.8
M^2, length	19	7.9	10.2	8.72	0.57	6.5
M^2, width	16	9.1	10.5	9.88	0.47	6.5
M^3, length	14	7.0	8.7	7.64	0.49	6.3
M^3, width	14	6.6	8.4	7.57	0.53	6.9

Table A-25. Summary statistics for *Phenacodus vortmani*, *Heptodon* zone, Bighorn Basin.

	N	Min	Max	Mean	SD	V
P_3, length	35	6.4	9.1	7.69	0.60	7.7
P_3, width	36	3.4	5.5	4.53	0.42	9.2
P_4, length	79	7.8	10.5	8.76	0.47	5.3
P_4, width	75	5.2	6.8	5.86	0.35	5.8
M_1, length	83	7.4	9.4	8.41	0.44	5.2
M_1, width trigonid	80	5.8	7.9	7.04	0.42	5.9
M_2, length	99	7.5	9.3	8.38	0.42	4.9
M_2, width trigonid	95	6.2	8.3	7.37	0.40	5.4
M_3, length	73	7.9	10.3	8.73	0.52	6.0
M_3, width trigonid	70	5.4	7.3	6.23	0.40	6.4
P^3, length	9	6.6	7.8	7.23	0.34	4.6
P^3, width	9	5.9	7.7	6.76	0.61	9.0
P^4, length	26	7.1	9.0	7.84	0.49	6.1
P^4, width	24	7.5	9.8	8.74	0.50	5.7
M^1, length	28	8.1	9.8	8.81	0.46	5.1
M^1, width	25	8.6	11.5	10.24	0.67	6.5
M^2, length	29	7.9	10.1	8.83	0.59	6.7
M^2, width	28	8.8	11.2	10.10	0.59	6.7
M^3, length	21	6.5	9.0	7.71	0.70	9.1
M^3, width	21	6.7	8.3	7.53	0.44	5.8

Table A-26. Summary statistics for *Phenacodus intermedius*, *Plesiadapis gingerichi* zone, Clarks Fork Basin.

	N	Min	Max	Mean	SD	V
P_3, length	7	10.1	11.0	10.40	0.32	3.0
P_3, width	7	6.1	7.1	6.71	0.40	5.9
P_4, length	13	9.7	12.4	11.16	0.68	6.1
P_4, width	15	7.3	9.1	8.32	0.60	6.4
M_1, length	11	10.9	12.5	11.82	0.49	4.2
M_1, width trigonid	14	8.7	10.6	9.78	0.52	5.3
M_2, length	13	11.1	13.5	12.26	0.66	5.3
M_2, width trigonid	14	9.9	12.0	11.05	0.59	5.3
M_3, length	17	10.6	13.9	12.19	0.94	7.7
M_3, width trigonid	17	8.3	10.1	9.20	0.53	5.8
P^3, width	1			8.4		
P^4, length	6	9.7	11.6	10.57	0.70	6.6
P^4, width	4	10.2	12.7	11.05	1.14	10.3
M^1, length	6	10.4	12.8	11.47	0.94	8.2
M^1, width	5	11.9	14.7	12.82	1.14	8.9
M^2, length	4	10.9	12.1	11.45	0.50	4.4
M^2, width	3	12.1	13.9	13.17	0.95	7.2
M^3, length	5	9.6	12.2	10.86	1.07	9.8
M^3, width	5	9.1	12.1	10.58	1.10	10.4

Table A-27. Summary statistics for *Phenacodus intermedius*, *Plesiadapis cookei* zone, Bighorn Basin.

	N	Min	Max	Mean	SD	V
P_3, length	18	10.2	12.1	10.93	0.58	5.3
P_3, width	22	5.4	8.1	6.87	0.60	8.7
P_4, length	33	10.2	13.5	11.93	0.82	6.9
P_4, width	34	7.5	10.1	8.62	0.65	7.5
M_1, length	44	11.1	14.0	12.36	0.70	8.1
M_1, width trigonid	40	9.3	11.6	10.25	0.56	5.5
M_2, length	44	11.2	14.3	12.76	0.66	5.1
M_2, width trigonid	47	9.6	12.9	11.28	0.78	6.9
M_3, length	41	11.4	15.2	13.13	0.86	6.5
M_3, width trigonid	41	8.4	10.7	9.78	0.59	6.0
P^3, length	12	9.5	12.1	10.73	0.69	6.4
P^3, width	14	8.9	11.4	9.88	0.74	7.4
P^4, length	21	9.2	11.6	10.67	0.65	6.1
P^4, width	24	9.0	13.1	11.52	0.86	7.5
M^1, length	20	10.7	14.5	12.33	0.94	7.6
M^1, width	22	11.8	16.3	13.83	1.14	8.2
M^2, length	29	10.9	16.1	13.21	1.03	7.7
M^2, width	29	12.4	15.7	14.28	0.90	6.3
M^3, length	38	10.2	14.0	11.73	0.85	7.2
M^3, width	40	8.8	14.2	10.95	1.04	9.5

Table A-28. Summary statistics for *Phenacodus intermedius, Phenacodus-Ectocion* zone, Bighorn Basin.

	N	Min	Max	Mean	SD	V
P_3, length	5	11.0	12.3	11.46	0.50	4.3
P_3, width	6	6.3	8.1	6.93	0.72	10.3
P_4, length	17	10.5	13.5	12.30	0.92	7.4
P_4, width	17	7.7	9.4	8.56	0.49	5.6
M_1, length	13	10.8	13.0	11.83	0.67	5.6
M_1, width trigonid	15	9.2	10.9	9.99	0.48	4.8
M_2, length	18	11.4	13.9	12.67	0.65	5.1
M_2, width trigonid	16	10.2	11.6	11.08	0.42	3.8
M_3, length	17	12.3	14.5	13.17	0.72	5.5
M_3, width trigonid	18	9.0	11.0	9.68	0.52	5.3
P^3, length	7	9.5	11.9	11.04	0.87	7.9
P^3, width	8	9.1	11.9	10.00	0.97	9.7
P^4, length	8	10.4	13.0	11.46	0.77	6.7
P^4, width	7	10.8	14.2	12.26	1.42	11.5
M^1, length	11	12.0	14.6	12.78	0.75	5.8
M^1, width	13	12.2	16.0	14.00	1.10	7.9
M^2, length	13	12.5	15.9	13.85	1.00	7.2
M^2, width	16	12.8	16.3	14.78	1.08	7.2
M^3, length	22	10.2	13.4	12.52	0.76	6.0
M^3, width	23	10.5	13.3	11.89	0.90	7.5

Table A-30. Summary statistics for *Phenacodus trilobatus*, Upper *Haplomylus-Ectocion* zone, Bighorn Basin.

	N	Min	Max	Mean	SD	V
P_3, length	11	11.3	12.1	11.61	0.28	2.4
P_3, width	11	6.4	7.6	6.97	0.42	5.9
P_4, length	26	11.6	14.0	12.47	0.57	4.5
P_4, width	34	7.7	9.8	8.82	0.55	6.2
M_1, length	43	11.2	14.0	12.57	0.69	5.5
M_1, width trigonid	43	9.3	12.4	10.68	0.71	6.6
M_2, length	58	11.9	14.7	13.03	0.59	4.5
M_2, width trigonid	57	10.0	13.2	11.83	0.71	6.0
M_3, length	57	11.4	15.6	13.55	0.96	7.1
M_3, width trigonid	62	8.3	11.8	10.27	0.86	8.3
P^3, length	10	9.7	12.4	11.02	0.76	6.9
P^3, width	10	8.0	11.0	9.69	1.07	11.0
P^4, length	8	10.6	11.8	11.26	0.42	3.6
P^4, width	13	11.0	12.6	11.85	0.56	4.7
M^1, length	15	12.2	15.3	13.51	0.90	6.6
M^1, width	13	13.1	16.0	14.60	0.93	6.3
M^2, length	14	12.7	15.7	14.01	0.81	5.7
M^2, width	12	13.8	16.7	15.17	0.77	5.1
M^3, length	26	10.6	15.0	12.87	1.08	8.4
M^3, width	26	10.3	13.7	12.02	0.90	7.4

Table A-29. Summary statistics for *Phenacodus intermedius*, Lower *Haplomylus-Ectocion* zone, Bighorn Basin.

	N	Min	Max	Mean	SD	V
P_3, length	15	8.8	12.2	10.28	0.93	9.0
P_3, width	20	4.7	7.5	6.03	0.58	9.6
P_4, length	38	9.4	12.7	11.02	0.73	6.6
P_4, width	42	6.5	8.6	7.53	0.46	6.0
M_1, length	41	9.6	13.2	10.92	0.65	5.9
M_1, width trigonid	38	8.0	10.6	9.02	0.56	6.2
M_2, length	49	10.1	12.5	11.41	0.64	5.6
M_2, width trigonid	51	9.0	11.8	10.31	0.61	6.0
M_3, length	50	10.0	13.7	11.64	0.90	7.7
M_3, width trigonid	54	7.6	10.6	8.74	0.71	8.0
P^3, length	5	7.9	10.8	9.32	1.06	11.3
P^3, width	5	6.9	9.6	8.36	0.97	11.6
P^4, length	8	8.9	11.3	9.79	0.88	8.9
P^4, width	9	9.0	11.5	10.27	0.80	7.8
M^1, length	20	10.3	13.0	11.57	0.73	6.3
M^1, width	20	11.4	14.0	12.52	0.81	6.4
M^2, length	22	10.6	12.8	11.76	0.73	6.1
M^2, width	18	11.5	14.5	12.82	0.76	5.9
M^3, length	22	9.5	12.6	11.10	0.84	7.5
M^3, width	22	8.2	12.0	10.26	0.94	9.2

Table A-31. Summary statistics for *Copecion brachypternus*, Lower *Haplomylus-Ectocion* zone, Bighorn Basin.

	N	Min	Max	Mean	SD	V
P_3, length	5	7.2	8.0	7.66	0.33	4.2
P_3, width	6	3.8	4.5	4.03	0.26	6.4
P_4, length	9	7.2	8.6	8.00	0.51	6.3
P_4, width	11	4.3	5.3	4.72	0.28	6.0
M_1, length	14	6.0	7.9	6.82	0.53	7.6
M_1, width trigonid	12	4.6	5.7	5.25	0.35	6.6
M_2, length	18	6.1	7.3	6.87	0.33	4.7
M_2, width trigonid	18	4.7	6.3	5.77	0.42	7.2
M_3, length	10	6.9	7.7	7.21	0.23	3.2
M_3, width trigonid	10	4.4	5.5	5.01	0.29	5.6
P^4, length	1			6.6		
P^4, width	1			7.0		
M^1, length	7	6.3	7.8	6.97	0.54	7.9
M^1, width	6	7.9	9.2	8.52	0.52	6.0
M^2, length	11	6.1	8.0	7.29	0.56	7.7
M^2, width	11	8.0	9.0	8.62	0.32	3.7
M^3, length	9	5.2	7.6	6.21	0.65	10.4
M^3, width	9	5.9	7.4	6.72	0.64	9.5

Table A-32. Summary statistics for *Copecion brachypternus, Bunophorus* zone, Bighorn Basin.

	N	Min	Max	Mean	SD	V
P_3, length	13	6.8	8.1	7.28	0.38	5.2
P_3, width	16	3.2	4.1	3.63	0.25	6.9
P_4, length	40	6.5	8.8	7.72	0.46	5.9
P_4, width	39	4.3	5.2	4.72	0.26	5.4
M_1, length	46	6.0	7.6	6.72	0.39	5.7
M_1, width trigonid	46	4.8	6.2	5.45	0.32	5.7
M_2, length	47	6.0	7.7	6.71	0.39	5.8
M_2, width trigonid	42	5.0	6.5	5.73	0.27	4.6
M_3, length	32	6.5	7.9	7.02	0.36	5.1
M_3, width trigonid	33	4.2	5.5	4.91	0.28	5.7
P^3, length	4	7.2	7.7	7.43	0.23	3.0
P^3, width	4	5.1	6.5	5.63	0.61	10.8
P^4, length	10	6.2	7.6	6.82	0.48	6.9
P^4, width	9	7.2	7.9	7.50	0.26	3.5
M^1, length	3	6.8	7.5	7.27	0.41	5.6
M^1, width	5	7.8	8.6	8.26	0.30	3.6
M^2, length	11	6.3	7.6	7.03	0.42	5.9
M^2, width	10	7.9	9.0	8.47	0.30	3.5
M^3, length	7	5.7	7.0	6.30	0.44	7.0
M^3, width	8	6.0	7.4	6.63	0.55	8.3

Table A-33. Summary statistics for *Copecion brachypternus, Heptodon* zone, Bighorn Basin.

	N	Min	Max	Mean	SD	V
P_3, length	1			7.5		
P_3, width	1			4.4		
P_4, length	4	6.9	8.3	7.87	0.66	8.3
P_4, width	5	4.4	5.3	5.96	0.40	7.9
M_1, length	8	6.7	7.5	6.98	0.28	4.0
M_1, width trigonid	8	5.2	5.9	5.60	0.20	3.6
M_2, length	11	6.3	7.6	6.93	0.42	6.0
M_2, width trigonid	10	5.5	6.4	5.95	0.25	4.1
M_3, length	9	7.1	8.0	7.50	0.34	4.4
M_3, width trigonid	10	4.5	5.4	5.07	0.27	5.2
P^4, length	1			6.4		
P^4, width	1			7.7		
M^2, length	3	6.9	7.6	7.27	0.36	4.8
M^2, width	2	8.3	9.1	8.70	0.57	6.5
M^3, length	4	5.8	6.9	6.48	0.48	7.4
M^3, width	4	5.8	7.4	6.80	0.74	11.0

Table A-34. Summary statistics for *Copecion davisi, Cantius torresi* zone, Bighorn Basin.

	N	Min	Max	Mean	SD	V
P_3, length	2	6.0	7.2	6.60	0.85	12.9
P_3, width	2	2.8	3.5	3.15	0.50	15.7
P_4, length	11	5.5	6.7	6.15	0.35	5.6
P_4, width	11	3.4	4.1	3.82	0.21	5.3
M_1, length	11	5.2	6.2	5.64	0.28	4.8
M_1, width trigonid	9	4.0	4.7	4.36	0.22	5.1
M_2, length	10	5.2	6.3	5.78	0.36	6.2
M_2, width trigonid	11	4.3	5.1	4.79	0.28	5.6
M_3, length	11	4.4	6.1	5.57	0.54	9.5
M_3, width trigonid	11	3.2	5.0	4.00	0.47	11.6
P^3, length	1			3.8		
P^3, width	1			2.2		
P^4, width	1			6.2		
M^1, length	3	5.8	6.3	6.10	0.27	4.3
M^1, width	3	6.6	7.4	7.07	0.42	5.9
M^2, length	5	5.4	6.5	5.96	0.41	6.8
M^2, width	4	6.2	7.6	6.98	0.59	8.5
M^3, length	6	4.4	5.6	4.88	0.43	8.7
M^3, width	6	4.6	5.9	5.20	0.42	8.1