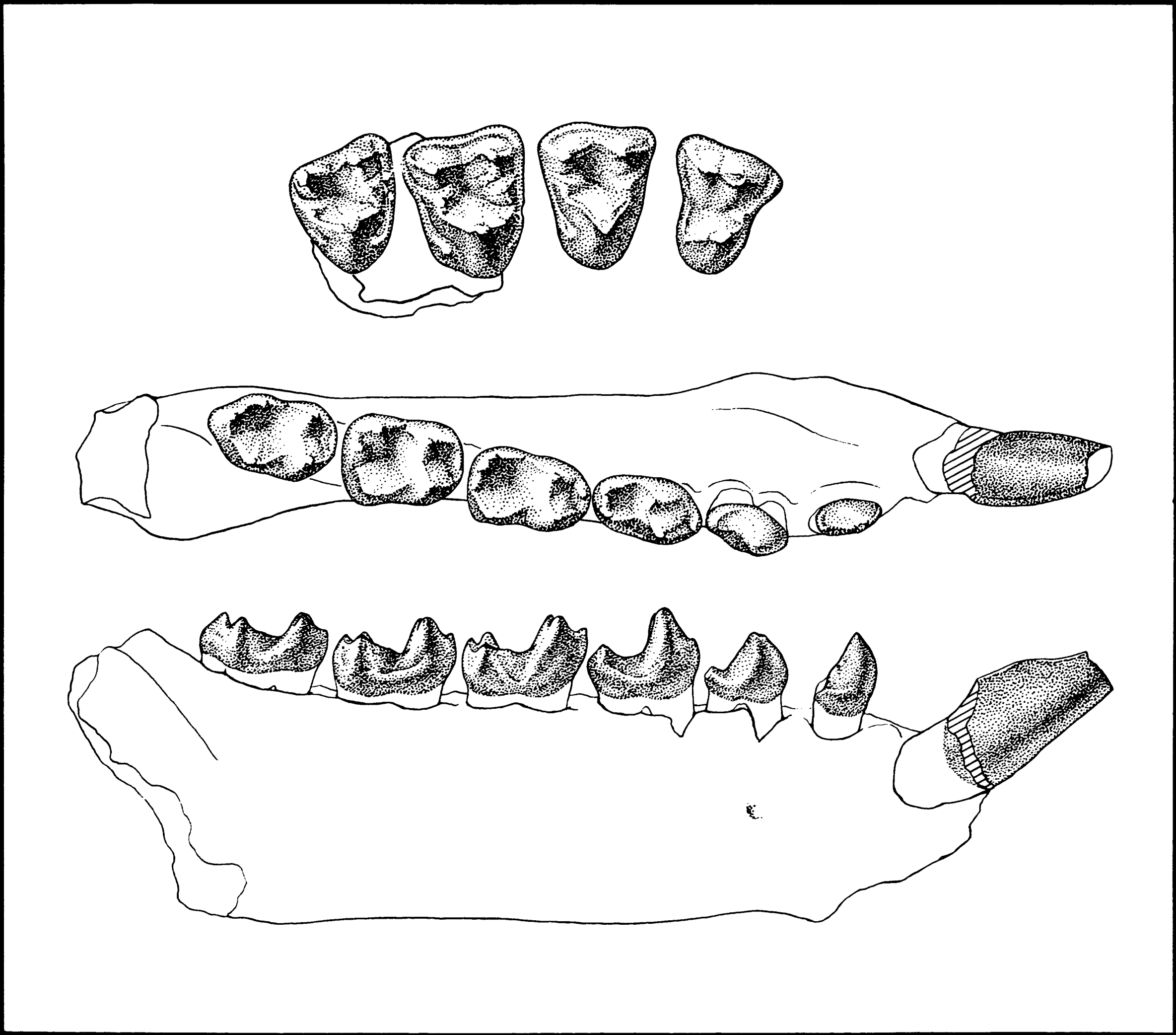
EVOLUTIONARY HISTORY OF MICROSYOPOIDEA (MAMMALIA, ?PRIMATES) AND THE RELATIONSHIP BETWEEN PLESIADAPIFORMES AND PRIMATES

GREGG F. GUNNELL



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ABSTRACT

Plesiadapiformes is the first group of primate-like mammals known in the fossil record. Plesiadapiformes first appear in the Paleocene (Puercan Land Mammal Age) in sediments of the Western Interior of North America. The relationship of Paleocene plesiadapiforms to Eocene primates of modern aspect (euprimates) and relationships among various families, genera, and species of plesiadapiforms are uncertain. In particular, the relationship of Microsyopoidea to plesiadapiforms has been questioned.

Morphological and functional studies of dental and cranial remains of plesiadapiforms presented in this study indicate that there is no direct relationship between plesiadapiforms and euprimates. Plesiadapiformes are retained, questionably, in the order Primates, based solely on gradistic considerations. Dental evidence suggests that plesiadapiforms are more closely related to fossil "dermopterans" (Plagiomenidae) than either group is to euprimates. Microsyopoids are distinctly primitive in a number of dental and cranial features, but are more closely related to plesiadapoids than to any other group.

Microsyopoidea is represented by two families: Paleocene Palaechthonidae (new family) and late Paleocene and Eocene Microsyopidae. Available evidence suggests that microsyopids are more closely related to palaechthonids than to any other group and can best be viewed as descendants of that group.

Microsyopidae and Paromomyidae survived well into the Eocene (Uintan Land Mammal age, late middle Eocene), while all other families of plesiadapiforms disappeared by the early Eocene (Wasatchian Land Mammal Age). Dental characteristics indicate that these two families specialized on diets different from those of euprimates (adapids and omomyids) and avoided direct competition with them.

Geographic distributions indicate that microsyopoids were members of a southern ecological community, while plesiadapoids were members of a northern ecological community. Paleotemperature reconstructions indicate that microsyopoids were the dominant plesiadapiform group during warm periods, while plesiadapoids dominated during cooler periods. A sudden warming event that occurred at the Clarkforkian-Wasatchian boundary contributed to the extinction of most plesiadapiform groups.

I
INTRODUCTION

The Paleocene and Eocene fossil record of the North American Western Interior includes a rich fauna of primate-like forms, generally referred to as the suborder or infraorder Plesiadapiformes. The first representative of this group, *Purgatorius*, is known from deposits in Montana that are approximately 65 million years old, while the last representatives appear in California in deposits 38 to 40 million years old. Late Paleocene and early Eocene representatives of the plesiadapiform radiation are also known from Europe.

Plesiadapiforms pose interesting questions concerning the origin of order Primates. Many authors consider some or all of this group as primates, which would place the origin of the order in the late Cretaceous of North America. Other authors deny primate status for some or all plesiadapiforms and suggest that primates may have originated more recently and in a different geographic setting, perhaps in the middle to late Paleocene of Africa, Asia, or India.

Plesiadapiformes are a common element of mammalian faunas in North America from the middle Paleocene through the late Paleocene and persist into and through most of the Eocene, although their diversity is reduced during the Eocene. Two superfamilies and six families are generally recognized in the Paleocene (see Figure 1): plesiadapoid Plesiadapidae, Paromomyidae, Carpolestidae, Picrodontidae, Saxonellidae, and microsyopoid Microsyopidae. These families represent approximately 20% of mammalian taxonomic diversity at the species level through most of the Paleocene (see Rose, 1981a,b). At certain localities in the later Paleocene they may represent as much as 40% to 45% of mammalian taxonomic specific diversity (perhaps due in part to sampling bias). In the earliest Eocene (Clarkforkian Land Mammal Age) plesiadapiforms still represent 15% to 20% of mammalian diversity. At the transition between the Clarkforkian Land Mammal Age and Wasatchian Land Mammal Age, two families (Microsyopidae and Paromomyidae) survive (see Figure 1). These archaic families represent only 1–2% of mammalian specific diversity in the early Eocene. These two families persist through most of the Eocene at these low diversities (or lower), finally disappearing near the end of Eocene.

This study has as its aim two major points. First, the relationship between Plesiadapiformes and Primates is examined. Relevant questions include: Are Plesiadapiformes themselves Primates? If so are they ancestral to other Primates? If not, what relationship, if any, do they have to the origin of the Primate order? Second, the relationships between various members within plesiadapiforms are examined, particularly relationships between the two families that survived into the Eocene. Relevant questions include: What are the systematic affinities of the various taxa that are included in plesiadapiforms? Why do most plesiadapiform families disappear at the Clarkforkian-Wasatchian boundary? Why do two families survive well into the Eocene?

Concerning the last question, the superfamily Microsyopoidea is examined in detail. Relationships among taxa included in this superfamily are discussed and their paleobiological attributes are examined. Paleobiological examination provides clues to the ecological attributes of these archaic taxa and suggest reasons that many microsyopoids survived well into the Eocene. In addition, paleogeographical distributions and paleoclimatological information are examined to provide further evidence concerning the questions posed above.

In the chapters that follow I examine the questions posed above in the plesiadapiform radiation. I find no evidence that plesiadapiforms are ancestral to primates of modern aspect (euprimates). Dental and paleoclimatic evidence provides plausible reasons why most plesiadapiforms failed to survive past the Clarkforkian-Wasatchian boundary. Dental evidence suggests that competition for food resources may have occured between many plesiadapiforms and rodents. Paleoclimatic evidence indicates initiation of warmer, more subtropical conditions at the beginning of the early Eocene, favoring plesiadapiform families associated with southern faunal communities (palaechthonids, new family, and microsyopids) and adversely effecting plesiadapiform families associated with northern faunal communities (plesiadapids and carpolestids). These conclusions are discussed more fully in the relevant chapters and in the final summary (Chapter VIII).

Abbreviations

Acronyms of institutions where specimens used in this study are housed.

AMNH—American Museum of Natural History (New York)

LACM—Los Angeles County Museum (Los Angeles)

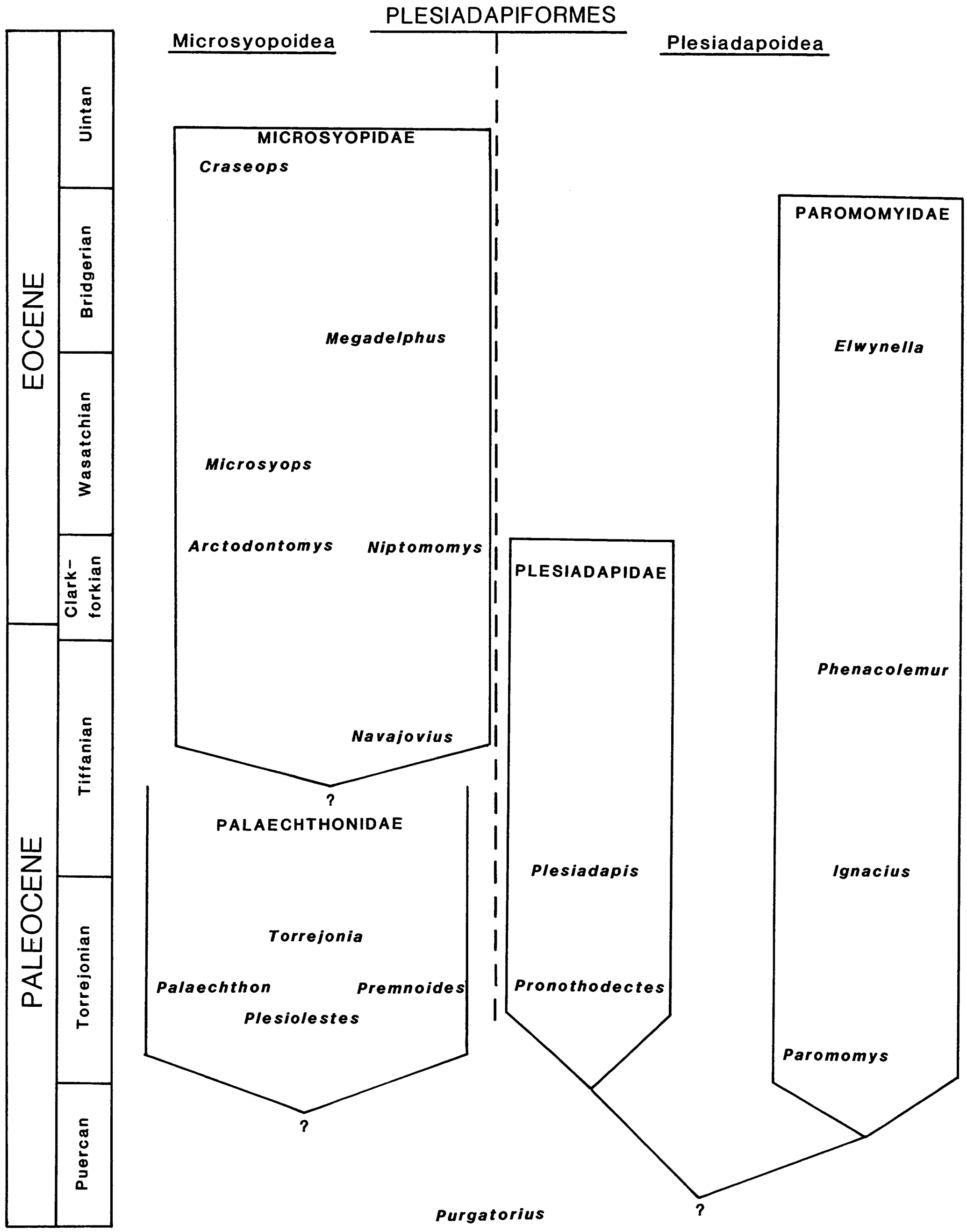

Figure 1. North American Plesiadapiform radiation, including some of the important taxa discussed here. Note the existence of three other families, Carpolestidae, Picrodontidae, and Saxonellidae, whose ranges are not depicted in this figure. Rectangles enclose probable ranges of families Microsyopidae, Palaechthonidae, Plesiadapidae, and Paromomyidae. Dashed vertical line separates the two superfamilies of plesiadapiforms relevant to this study. Vertical scale represents Paleocene and Eocene epochs and the Land Mammal Ages included in them.

MCZ—Museum of Comparative Zoology, Harvard University (Cambridge)
PU—Princeton University (Princeton) (Now housed at Yale Peabody Museum - YPM-PU)
UCM—University of Colorado Museum (Boulder)
UCMP—University of California, Museum of Paleontology (Berkeley)
UKMNH—University of Kansas, Museum of Natural History (Lawrence)
UM—University of Michigan, Museum of Paleontology (Ann Arbor)
USGS—United States Geological Survey (Denver)
USNM—United States National Museum (Washington, D.C.)
UW—University of Wyoming (Laramie)
YPM—Yale Peabody Museum (New Haven)

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II
STRATIGRAPHY AND BIOCHRONOLOGY

In this chapter I discuss stratigraphy and biochronology, providing a brief history and a summary of stratigraphic methods. The importance of stratigraphy lies in its usefulness in reconstructing an independent, relative time scale separate from fossil evidence. When this is done, evolutionary relationships can often be traced through time.

Stratigraphy provides useful information in the study of evolutionary history. Three aspects of paleontology are closely tied to stratigraphy: 1) stratigraphy provides an independent relative time frame over which fossil taxa can be arrayed; 2) the component of time provided by stratigraphy allows for the study of phylogenetic relationships between taxa because it is often possible to trace these relationships through time; 3) the independent time element allows for the development of biostratigraphic chronologic units based on taxa preserved within a given time segment. Biostratigraphic units can prove useful in correlating stratigraphic sequences from differing geographic areas.

Concerning point 2 above, it is often possible to trace relationships between ancestor and descendant taxa because of continuity of descent. Under the Darwinian model, evolutionary change is continuous between ancestral and descendant species, and if fossil specimens are arrayed through time, the nature of this continuity should be evident. When gaps appear in the fossil record because of geologic phenomena, continuity of descent is not disrupted, but only unrepresented in the geologic record (under the puncuated equilibrium model these gaps represent real events; see Eldredge and Gould, 1972).

Steno (1669) described the principle of superposition. He noted that in a normal sedimentary system the oldest rock units would be those that were deposited first, with younger units being deposited on top of older units. Thus in an undisturbed sedimentary sequence the oldest sediments would be at the bottom, with successively younger sediments layered on top. This seems self-evident today, but at the time was a major advance in the study of earth history, and was the beginning of the study of stratigraphy (many others before Steno had recognized the origin of sedimentary rocks, including the great Greek historian Herodotus and the Italian artist and scientist Leonardo da Vinci, but no one had so explicitly considered the temporal relationships between sedimentary units).

In the early 1800's William Smith, while preparing a geologic map of England, noted that faunas from successively younger strata were different from those below them (and above them). Smith (1815, 1816) published his findings, developing the principles of faunal correlation and faunal succession. By faunal correlation it is possible to correlate stratigraphic units containing the same fossils and infer that they are of the same relative age. This was the first step in recognizing chronological zones within stratigraphic units.

The early Cenozoic has been divided into Paleocene and Eocene epochs. Each of these epochs has been further subdivided into North American Land-Mammal Ages. The Paleocene is divided into three Land-Mammal Ages, Puercan (early Paleocene), Torrejonian (middle Paleocene), and Tiffanian (late Paleocene). The Clarkforkian Land-Mammal Age spans the boundary between the Paleocene and Eocene (Rose, 1981a). The remainder of the Eocene has been divided into four Land-Mammal Ages, Wasatchian, Bridgerian, Uintan, and Duchesnean, from early to late Eocene, respectively.

Gingerich (1975, 1976) developed a series of biochronological zones for the middle and late Paleocene (Torrejonian and Tiffanian Land-Mammal Ages) in the Bighorn and Clark's Fork Basins of Wyoming. Recent work (see Schankler, 1980, Rose, 1981, Gingerich, 1983, Gingerich, Rose, and Krause, 1980, Stucky, 1984a-b, and Woodburne, 1987) has led to the refinement of biochronological zones for North American Paleocene and Eocene faunas.

In the Paleocene, Gingerich (1975) recognized eight biostratigraphic units or zones in the Paleocene, based on species of plesiadapiforms of the family Plesiadapidae. Establishment of these biochronological zones was a relatively simple process of stacking successive stratigraphic intervals in their proper sequence based on the principle of superposition. Once this was done through a number of stratigraphic intervals from different geographic areas, correlating zones based on the species of plesiadapids from each level was possible. The result was a sequence of biochronological units with a distinctive plesiadapid taxon representative of each biochronological zone. Figure 2 presents the biochronological zones for the middle and late Paleocene, and early Eocene based on plesiadapid plesiadapiforms (Gingerich, 1975; Archibald, et al., 1987).

Rose (1980, 1981a) developed a similar biostratigraphic zonation for the Clarkforkian Land-Mammal Age (latest Paleocene-earliest Eocene), again basing it for the most part on plesiadapid plesiadapiforms, one of the more common elements of Clarkforkian faunas. The first two zones

Epoch	Biochronological Zone	Land Mammal Age
EOCENE	Phenacodus-Ectocion Acme-Zone (Cf3)	LATE CLARKFORKIAN
	Plesiadapis cookei Lineage-Zone (Cf2)	MIDDLE CLARKFORKIAN
PALEOCENE	Rodentia/P. cookei Interval-Subzone (Cf1)	EARLY CLARKFORKIAN
	P. gingerichi/Rodentia Interval-Subzone (Ti6)	LATE TIFFANIAN
	P.simonsi/P.gingerichi Lineage-Zone (Ti5)	
	P.churchilli/P.simonsi Lineage-Zone (Ti4)	
	P.rex/P.churchilli Lineage-Zone (Ti3)	MIDDLE TIFFANIAN
	P.anceps/P.rex Lineage-Zone (Ti2)	EARLY TIFFANIAN
	P.praecursor/P.anceps Lineage-Zone (Ti1)	
	Pantolambda/ P.praecursor Interval-Zone (To3)	LATE TORREJONIAN
	Tetraclaenodon/ Pantolambda Interval-Zone (To2)	MIDDLE TORREJONIAN

Figure 2. Biochronological zones for middle Paleocene through earliest Eocene (Torrejonian through Clarkforkian Land Mammal Ages, adapted from Rose, 1981a, and Archibald, et al., 1987).

of the Clarkforkian were defined on the first appearance and presence of two successive *Plesiadapis* species, *P. gingerichi* and *P. cookei*. The last Clarkforkian zone is defined by the absence of *P. cookei* and the abundance of two phenacodontid condylarths, *Phenacodus* and *Ectocion*. Archibald, et.al. (1987) have defined Rose's three zones as the Rodentia/*Plesiadapis cookei* Interval-Subzone (Cf1), the *Plesiadapis cookei* Lineage Zone (Cf2), and the *Phenacodus-Ectocion* Acme Zone (Cf3). The *Plesiadapis gingerichi*/Rodentia Interval-Subzone is now placed in the latest Tiffanian (Ti6).

Gingerich and Simons (1977) studied the adapid primate *Cantius* (*"Pelycodus"* of their study) from the Wasatchian Land Mammal Age and suggested subdivision of that age on the basis of *Cantius* species, into five biochronological zones. More recently, Gingerich (1983a) has subdivided the Wasatchian into seven biochronological zones based on species of adapid primates, perissodactyls and artiodactyls.

Schankler (1980) also studied the faunas of the Wasatchian in the Bighorn Basin of Wyoming. Instead of looking at single taxa, he concentrated on patterns of change in faunal assemblages and was able to divide the Wasatchian into four parts based on these faunal changes. He studied the frequencies of local origination (appearances) and local extinctions (disappearances) of species through the lower and middle portions of the Wasatchian, noting three periods of distinct faunal change. He termed each of these faunal changes a "biohorizon," in sequence from oldest to youngest, biohorizons A, B, and C. Biohorizon A is characterized by the extinction or disappearance of eight species and the appearance of seven new species at or slightly after this level. The other two biohorizons also represent periods of high faunal turnover. Biohorizon B is marked by 13 disappearances and 6 appearances, while Biohorizon C is marked by 6 new occurrences and perhaps 3 to 4 disappearances.

In the cases of both Gingerich and Simons (1977) and Schankler (1980), stratigraphic sections were first measured in the field relating all fossil localities on their superposition, and then patterns of evolution in a single taxon (adapid primates in the case of Gingerich and Simons) or faunal assemblages (in the case of Schankler) were studied in stratigraphic context.

Stucky (1984a, 1984b) studied the later portion of the Wasatchian (the Lostcabinian subage) and the early Bridgerian in the Wind River Basin in Wyoming and developed biostratigraphic units based on the occurrence of characteristic faunal assemblages in each zone. He subdivided the late Wasatchian and early Bridgerian into the *Lambdotherium* Range Zone and the *Paleosyops borealis* Assemblage Zone. West, et.al. (1987) have further refined the biostratigraphy of the whole of the Eocene.

In all of these cases, the methodologies differ slightly from one another based on the density of the fossil record, the occurrence of fossil localities, and the author's approach. One type of fossil locality is prevalent in the Paleocene. These are rich fossil quarries that have highly concentrated bone deposits. This type of deposit is advantageous because a great number of specimens from a single taxon may be present in each quarry. However, rich assemblages such as those of Cedar Point Quarry or Rock Bench Quarry (see below) are not common, and each quarry may be separated from successive ones by a thick stratigraphic sequence that is essentially non-fossiliferous or only poorly represented by fossil taxa. For example, in the Clark's Fork Basin, there are essentially six rich fossil localities in the Paleocene including Rock Bench Quarry, Cedar Point Quarry, Witter Quarry (previously known as Croc Tooth Quarry), Divide Quarry, Long Draw Quarry, and Princeton Quarry. Stacking these localities by stratigraphic superposition produces a sequence with Rock Bench Quarry on the bottom (Torrejonian), followed by Cedar Point Quarry, then Witter, Long Draw and Divide Quarries at essentially the same level, and Princeton Quarry (late Tiffanian) on top. Most of these quarries are separated by several hundred meters of sediment (except for the three of similar age) and often by many kilometers geographically. Each has a distinctive plesiadapid plesiadapiform characteristic of it and each represents a given plesiadapid biostratigraphic zone. Biostratigraphic zones are thus defined on isolated pockets of rich fossil assemblages, and the time ranges of individual species are virtually unknown. For instance, all localities with *Plesiadapis rex* from North America (there are many ranging from Canada to Texas) are correlated together in the *Plesiadapis rex* zone. However, within that zone it is impossible to determine whether the localities are early or late in the *Plesiadapis rex* zone. Paleocene localities can be allocated to biostratigraphic zones but the temporal extent of these zones remains difficult to define.

The Clarkforkian has a similar problem, because of the lack of rich fossil localities. In the Clark's Fork Basin there is a thick (540 meters) and essentially continuous stratigraphic section throughout the Clarkforkian Land Mammal Age. Fossil localities are spread throughout this section, but very few of these localities are represented by abundant fossil remains. Plesiadapids are relatively common in early and middle Clarkforkian assemblages yet are not very abundant at any given locality. *Plesiadapis cookei* is relatively common, but there are only three localities where it is represented by 10 or more specimens. Again, as in the Paleocene, the precise phylogenetic relationships between biochronologically relevant species are unknown because the sampling is too poor to define the nature of the transition between species. Clarkforkian localities in the Clark's Fork Basin come from a geographically continuous stratigraphic section. This section has been measured and it is possible to define where specimens come from within each biochronological zone. This is an improvement over Paleocene biostratigraphic zones because some indication of relative durations of Clarkforkian biostratigraphic zones is given. However, the fossil evidence is not complete enough to indicate the nature of the faunal boundaries between these zones and somewhat arbitrary stratigraphic levels must be chosen to define these boundaries based on the first and last appearances of the various taxa used to define the zones.

The Wasatchian Land-Mammal Age presents a slightly different problem. In the Clark's Fork Basin and the Bighorn Basin the sediments are thick and relatively continuous through the early and middle Wasatchian. Fossil localities have been stacked on the basis of stratigraphic superposition and sections measured through these sequences to assign localities to given meter levels as in the Clarkforkian sections. However, fossil localities in the Wasatchian are much more fossiliferous and preserve a great many more specimens. In this case the boundaries between fossil species are often difficult to determine (see Gingerich, 1976, 1985; Gingerich and Simons, 1977) and an arbitrary stratigraphic level may be chosen to divide two chronospecies. Studying faunal assemblages alleviates this problem slightly because boundaries are based on more than one species, but this results (usually) in less finely divided sections, because significant, recognizable horizons of faunal turnover may be less common than speciation events. For instance between Schankler's Biohorizons B and C, Gingerich (1983a) recognizes two distinct biochronological zones based on different species of the equid *Hyracotherium* (*H. aemulor* and *H. pernix*).

Figure 3 summarizes biostratigraphic information from the above discussion and presents the biostratigraphic terminology used in this study. I have used the terminology developed by Archibald, et al. (1987) for the middle and late Paleocene (Torrejonian and Tiffanian) and for the Clarkforkian (see Figure 2).

The Wasatchian Land Mammal Age can be divided into eight zones (Wa0-Wa7, see Gingerich, 1989). Wasatchian zone Wa0 is equivalent to early Sandcouleean. I propose the name *Cantius torresi* Assemblage-Zone for this sequence. It can be characterized by the first appearance of the genus *Cantius*, as well as the first appearance of a number of other genera typical of the Wasatchian (see Gingerich, 1989). Wa1 (middle Sandcouleean), here termed the *Cantius torresi*/*Cantius ralstoni* Lineage-Zone, is characterized by the first appearance of *Cantius ralstoni*, *Diacodexis metsiacus* (artiodactyl), *Haplomylus speirianus* (condylarth), and the genus *Homogalax* (perissodactyl). Wa2 (late Sandcouleean), termed the *Cantius ralstoni*/*Cantius mckennai* Lineage-Zone, is characterized by the first appearance of *Cantius mckennai*, and the carnivore, *Miacis deutschi*. These zones (Wa0-Wa2) make up the early Wasatchian.

Wa3 (early Graybullian), termed the *Cantius mckennai*/*Cantius trigonodus* Lineage-Zone, is characterized by the first appearance of *Hyracotherium aemulor* and *Homogalax protapirinus* (perissodactyls), *Esthonyx bisulcatus* (tillodont), *Hyopsodus latidens* (condylarth), and *Miacis exiguus* and *Vassacyon promicrodon* (carnivores). It is also characterized by the last appearance of *Cantius mckennai*. It appears that *C. mckennai* and *C. trigonodus* (called *Cantius frugivorus* by Beard, 1988) are chronospecies of the same lineage, with *C. mckennai* gradually giving rise to *C. trigonodus* (Gingerich and Simons, 1977). If this is the

Epoch	Age	Zone	Terminology Used/ Proposed Here	Alternate Zone Terminology		
EOCENE	Uintan	Ui2	Camelid-Canid Appearance-Zone	Uinta C	Late Uintan	
		Ui1	Epihippus Assemblage-Zone	Uinta A-B	Early Uintan	
	Bridgerian	Br3	Microsyops annectens Assemblage-Zone	Bridger C-D	Late Bridgerian	Twinbuttean
		Br2	Microsyops elegans Assemblage-Zone	Bridger B	Middle Bridgerian	Blacksforkian
		Br1	P. borealis Assemblage-Zone	Bridger A	Early Bridgerian Gardnerbuttean	
	Wasatchian	Wa7	Lambdotherium Range-Zone	Lostcabinian	Late Wasatchian	
		Wa6	Heptodon Interval-Zone	Lysitean		
		Wa5	Bunophorus Interval-Zone	Late Graybullian	Middle Wasatchian	
		Wa4	C.trigonodus/abditus Lineage-Zone	Middle Graybullian		Upper Haplomylus-Ectocion Range Zone
		Wa3	C.mckennai/trigonodus Lineage-Zone	Early Graybullian		
		Wa2	C.ralstoni/mckennai Lineage-Zone	Late Sandcouleean	Early Wasatchian	Lower Haplomylus-Ectocion Range Zone
		Wa1	C.torresi/ralstoni Lineage-Zone	Middle Sandcouleean		
		Wa0	Cantius torresi Assemblage-Zone	Early Sandcouleean		
	Clarkforkian	Cf3	Phenacodus-Ectocion Acme-Zone		Late Clarkforkian	
		Cf2	Plesiadapis cookei Lineage-Zone		Middle Clarkforkian	
PALEOCENE		Cf1	Rodentia/P.cookei Interval-Subzone		Early Clarkforkian	
	Tiffanian	Ti6	P.gingerichi/Rodentia Interval-Subzone		Late Tiffanian	
		Ti5	P.simonsi/gingerichi Lineage-Zone			
		Ti4	P.churchilli/simonsi Lineage-Zone			
		Ti3	P.rex/churchilli Lineage-Zone		Middle Tiffanian	
		Ti2	P.anceps/rex Lineage-Zone		Early Tiffanian	
		Ti1	P.praecursor/anceps Lineage-Zone			
	Torrejonian	To3	Pantolambda/P.praecurs Interval-Zone	Pantolambda Zone	Late Torrejonian	
		To2	Tetraclaen./Pantolambda Interval-Zone	Deltatherium Zone	Middle Torrejonian	
		To1	Periptychus/Tetraclaen. Interval-Zone	Dragonian	Early Torrejonian	

Figure 3. Summary of biostratigraphic terminology. Verticle divisions represent Paleocene and Eocene Epochs, North American Land Mammal Ages, and biochronological divisions within Land Mammal Ages. See text for further discussion (adapted from Gingerich, 1983, Archibald, etal., 1987, West, etal., 1987).

case, an arbitrary boundary between the two species must be chosen. It is convenient to choose the boundary between Wasatchian zones Wa3 and Wa4.

Wa4 (middle Graybullian), termed the *Cantius trigonodus/Cantius abditus* Lineage-Zone is characterized by the first appearance of *Hyracotherium pernix*, *Microsyops angustidens* (?primate), and the carnivore genus *Vulpavus*. It also is characterized by the last appearance of *Cantius trigonodus*. As in the case of *C. mckennai* and *C. trigonodus*, *C. trigonodus* and *C. abditus* also appear to be chronospecies of a single lineage. Again, a convenient boundary is that between Wasatchian zones Wa4 and Wa5.

Wa5 (late Graybullian), termed the *Bunophorus* Interval Zone (Schankler, 1980) is characterized by the first appearance of the artiodactyl *Bunophorus etsagicus* (may be present in the latest portion of Wa4 according to Schankler, 1980). It is also characterized by the first appearance of *Microsyops cardiorestes* and the presence of *Cantius abditus* throughout the interval. Wasatchian zones Wa3 through Wa5 constitute the middle Wasatchian.

Wa6 (Lysitean), termed the *Heptodon* Range-Zone (Schankler, 1980) is characterized by the first appearance of the perissodactyl *Heptodon*. Other taxa characteristic of this zone include *Chriacus gallinae* (condylarth), *Anacodon ursidens* (condylarth), *Microsyops latidens*, and *Hyopsodus powellianus*.

Wa7 (Lostcabinian), termed the *Lambdotherium* Range-Zone (Stucky, 1984a,b) is characterized by the first appearance of *Lambdotherium popoagicum* (perissodactyl), and also includes *Loveina zephryi* (primate), and *Hyopsodus walcottianus* (Stucky, 1984a). Wasatchian zones Wa6 and Wa7 constitute the late Wasatchian.

I have divided the Bridgerian into three zones, Br1-Br3. Br1, termed the *Paleosyops borealis* Assemblage-Zone (Stucky, 1984a,b) is characterized by the first appearance of the perissodactyl *Paleosyops borealis*. Other taxa typical of Bridger zone Br1 include *Megadelphus lundeliusi* (?primate), *Huerfanius* and *Hyrachyus* (perissodactyls), and *Notharctus* sp. (primate). I have included both the Gardnerbuttean Land Mammal Age (see Robinson, 1966 and Stucky, 1984a,b) and Bridger A (McGrew and Sullivan, 1970) in Bridger zone Br1. The relationship between Gardnerbuttean aged faunas and those of Bridger A are not yet clear. The Bridger A fauna is similar to that of the Gardnerbuttean, but also has some typical Bridger taxa as well (such as the primate *Anaptomorphus* and the creodont *Proviverra*). Further work is needed to clarify the relationships between these faunal zones and later Bridger faunas.

Bridger zone Br2, termed the *Microsyops elegans* Assemblage-Zone is characterized by the first appearance of *Microsyops elegans*. Other first appearances in Br2 include *Tillodon* (tillodont), *Patriofelis* (creodont), *Palaearctomys* (rodent), *Tetrapassalus* and *Metacheiromys* (edentates).

Bridger zone Br3, termed the *Microsyops annectens* Assemblage-Zone is characterized by the first appearances of *Microsyops annectens*, *Hemiacodon gracilis* (primate), and *Hyopsodus lepidus*. This zone is also characterized by the presence of abundant uintatheres (West, et al., 1987). Uintatheres are nearly completely absent in Bridger zones Br1 and Br2.

I have divided the Uintan Land Mammal Age into two zones, Ui1 and Ui2. Ui1, here termed the *Epihippus* Assemblage-Zone includes Uinta A and B (West, et al., 1987). It is characterized by the first appearance of the perissodactyls *Epihippus*, *Prothyracodon*, *Amynodon*, and *Triplopus*, the artiodactyls *Protoreodon* and *Protylopus*, and the primates *Ourayia* and *Macrotarsius*. Ui1 faunas are found in the Wagonhound Member of the Uinta Formation in Utah, the later Washakie Formation in the Washakie Basin in Wyoming, the lower Tepee Trail Formation in the Wind River Basin, Wyoming, the Poway Local Fauna in the Poway Conglomerate in California, and the lower Vieja Formation in Texas (Black and Dawson, 1966).

Uinta zone Ui2, here termed the Camelid-Canid Appearance-Zone is characterized by the first appearance of camels (*Poebrodon*) and canids (*Procyonodictis*). Lagomorphs (*Mytonolagus*) also appear in Ui2. Other characteristic taxa include the erinaceid *Ankylodon*, the soricid *Domnina*, the eomyid *Protadjidaumo*, the apternodontid *Oligoryctes*, and the microsyopid *Craseops*. Ui2 faunas are found in the Myton Member of the Uinta Formation in Utah, the Badwater fauna in the Wind River Basin, the Tapo Ranch fauna of the Sespe Formation in California, and perhaps the Colmena Local Fauna in Texas.

III
PALEOCENE PLESIADAPIFORMES OF THE SUPERFAMILIES MICROSYOPOIDEA AND PLESIADAPOIDEA

North American Paleocene plesiadapiforms have a relatively long (approximately 30 million years) and complex history. The paleontological literature is filled with wide-ranging discussions of this radiation. There is disagreement about many aspects of plesiadapiform history. Systematic questions center around which (if any) plesiadapiform taxa should be included within the order Primates. This, of course, stems from differing ideas on the combinations of characteristics that constitute a primate (a situation which exists even in the systematics of modern taxa, where tree shrews are still of uncertain status).

A related question concerns the origins of the group. Questions of the phylogenetic relationships among taxa and between them and later Eocene primates also remain. Paleobiological questions abound as well. What was the diet of these taxa; were they arboreal or terrestrial (or somewhere in between); nocturnal or diurnal; gregarious or solitary? These are just a few of the topics which have been addressed in the past.

This chapter is divided into three parts: 1), a detailed examination of the group previously referred to as Microsyopidae or Paromomyidae will be presented, including a revision of the systematics of these taxa; 2), an examination of the geographical distribution of the above taxa will be given in an attempt to clarify origins and relationships between them; and 3), a detailed review of cranial and postcranial elements will be given to address questions of their affinities to primates and their paleobiological attributes.

Systematics of Palaechthonidae and Paromomyidae

The North American Paleocene genera generally recognized as primates today (see Martin, 1972; Cartmill, 1972, Wible and Covert, 1987, for opposing viewpoints) include the plesiadapids *Plesiadapis*, *Chiromyoides*, *Nannodectes*, and *Pronothodectes*; the carpolestids *Elphidotarsius*, *Carpodaptes*, and *Carpolestes*; the paromomyids *Paromomys*, *Phenacolemur*, and *Ignacius*; the paromomyids or microsyopids *Purgatorius*, *Palaechthon*, *Plesiolestes*, *Torrejonia*, *Palenochtha*, *Navajovius*, and *Micromomys*; and the picrodontids *Picrodus*, *Zanycteris*, and *Draconodus*. Insectivore families which seem to have reached a similar grade (see MacPhee, Cartmill, and Gingerich, 1983) to that of early primate groups include Apatemyidae, Mixodectidae, and Tupaiidae (although definitive tupaiids are unknown from Paleocene or Eocene sediments). Fossil dermopterans also represent an adaptive plateau similar to that of plesiadapiforms.

In this section I will focus on those genera that comprise the Paromomyidae (Szalay and Delson, 1979) or Paromomyidae and Microsyopidae (Gingerich, 1976; Bown and Rose, 1976). The other North American Paleocene families have been dealt with extensively elsewhere. For detailed studies of Plesiadapidae see Gingerich (1976); for Carpolestidae see Rose (1975b); and for Picrodontidae see Szalay (1968).

Systematic Paleontology

Class MAMMALIA Linnaeus, 1758
Subclass THERIA Parker and Haswell, 1880
Infraclass EUTHERIA Gill, 1872
Order PRIMATES? Linnaeus, 1758
Suborder PLESIADAPIFORMES? Simons and Tattersall, 1972
Superfamily ?

Family Purgatoriidae, new rank

Type Genus.—Purgatorius.

Distribution.—Puercan, early Paleocene, Tullock Formation, Garfield County, Montana; ?Simpson Quarry, eastern Crazy Mountain Basin, Montana.

Emended Diagnosis.—Purgatoriids, represented by the single genus *Purgatorius*, are the most primitive plesiadapiforms known, dentally. They can be characterized as follows: 1) primitive lower dental formula of 3–1–4–3; 2) P_2 double-rooted; 3) canine large; 4) P_4 trigonid with distinct paraconid, no metaconid; 5) P_4 talonid rather weak with weak hypoconid; 6) no mesoconid on molars; 7) paraconids distinct on all molars; 8) M_{2-3} trigonids only very slightly compressed antero-posteriorly; 9) molar trigonids relatively high compared to talonids and only slightly anteriorly inclined; 10) talonids less transverse than trigonids; 11) molar hypoconulids weak, with shallow hypoconulid notch; 12) postprotocingulum variable on upper molars (sometimes present, sometimes absent); 14) incisors not markedly procumbent; 15) distinct metacone on P^4; 16) conules present on upper molars.

Discussion.—The position of *Purgatorius* has been much debated. When first described (Van Valen and Sloan, 1965), it was placed in Paromomyidae. Clemens (1974) also concluded that it was best viewed as a paromomyid, as do Szalay and Delson (1979), while Gingerich (1976) views it as a primitive microsyopid. These views are not dissimilar as paromomyids defined by Van Valen and Sloan (1965), Szalay and Delson (1979), and Clemens (1974) do not differ (except in included genera) from the concept of microsyopids held by Gingerich (1976). Later Bown and Rose (1976) and Kielan-Jaworowska, Bown, and Lillegraven (1979), included *Purgatorius* in plesiadapiforms, *incertae sedis*, recognizing its primitive nature and the lack of shared and derived characters with any later paromomyid. Savage, Russell, and Waters (1977) also recognize the primitive nature of *Purgatorius*, using it as a "model of primitiveness," with which to compare early Eocene taxa.

Examining the above characteristics suggests that *Purgatorius* retains many primitive eutherian characters, while possessing some derived features that are shared with later plesiadapiforms. The 3–1–4–3 dental formula is clearly a primitive character shared by many primitive eutherians, as is a double-rooted P_2 and a rather large canine. However, it is difficult to know how large the canine was, as it is only represented by alveoli in the specimens presently described. Savage, Russell, and Waters (1977) report that the canine (from alveolus measurements) is as large as any of the lower incisors, while Kielan-Jaworowska, Bown, and Lillegraven (1979), suggest that I_1 may be larger than the canine. Judging from alveolus size (on the one published specimen to preserve this feature) the canine was clearly larger than P_1, but probably about the same size as P_2 or slightly larger. I cannot judge its size relative to the incisors.

The fourth premolar shows specializations towards middle Paleocene plesiadapiforms. The trigonid is dominated by the protoconid, and there is no metaconid (some specimens show a thickening of enamel in this region, Clemens, 1974). The paraconid of P_4 is prominent and unlike any other eutherians (such as *Procerberus* and *Protungulatum*), the paraconid originates along the margin of the anterior flank of the protoconid, not from the base of the tooth (i.e., in *Purgatorius* the paraconid was not of cingular origin, see Savage, Russell, and Waters, 1977). However, a strong paraconid on P_4 is not shared with any of the middle Paleocene plesiadapiforms (most have no paraconid or only a fold of enamel forming a crest descending the anterior flank of the protoconid), and thus is probably an autapomorphous character state in *Purgatorius*. The development of a small talonid on P_4 foreshadows the more derived condition seen in palaechthonids.

The absence of a mesoconid is likely primitive, however, some *Procerberus* specimens possess a mesoconid (or an analogous structure), suggesting that morphocline polarities are difficult to assign for this character and limiting its taxonomic usefulness. Distinct paraconids on all molars are probably primitive and are shared with some middle and later Paleocene taxa (most notably *Palenochtha* and *Navajovius*). However, the rather unique anterior folding of the paraconid (especially strong on M_{2-3}) seen in *Purgatorius* may also be autapomorphic. In many ways this paraconid structure is suggestive of apatemyid insectivores. The anterior inclination of the molar trigonids (although slight) is reminiscent of later paromomyids and palaechthonids, as is the development of a hypoconulid. The shallow notch between the protoconid and metaconid on lower molars is probably primitive.

The variable presence of a postprotocingulum on upper molars foreshadows the characteristic presence of this feature in later Paleocene plesiadapiforms. A distinct metacone on P^4 is probably a primitive character.

The absence of any shared and derived characters consistent with paromomyids or palaechthonids (as here constituted) precludes the possibility of including *Purgatorius* in either of these families. I prefer to place *Purgatorius* in its own family, Purgatoriidae. Its primitive characters seem to suggest a closer relationship with Microsyopoidea than with Plesiadapoidea, as generally speaking, microsyopoids are distinctly primitive, while plesiadapoid families are typified by dental specializations. *Purgatorius* serves as a useful model for the ancestral morphotype of later palaechthonids (perhaps for plesiadapids, paromomyids, picrodontids, and carpolestids, as well).

Recently, Buckley (1988) has noted the presence of a *Purgatorius*-like taxon from Simpson Quarry in the Crazy Mountain Basin. Buckley (1988) feels that this taxon shares many plesiadapiform features and may provide further evidence for the origins of this group.

Suborder PLESIADAPIFORMES Simons and Tattersall, 1972
Superfamily Plesiadapoidea Trouessart, 1879
Family Paromomyidae (Simpson, 1940)

Type Genus.—Paromomys

Included Genera.—Paromomys, Phenacolemur, Ignacius, Elwynella.

Emended Diagnosis.—Paromomyids are characterized by the following: 1) I_1 pointed, procumbent, slender, not lanceolate (although this tooth remains unknown in *Paromomys*); 2) P_4 generally premolariform (although may be enlarged); 3) P_4 metaconid absent; 4) paraconids incipient to absent on M_{2-3}; 5) M_{2-3} molar trigonids antero-posteriorly compressed; 6) molar trigonids strongly inclined anteriorly; 7) hypoconulid absent on M_{1-2}; 8) upper molar conules absent to very weak; 9) upper molar cristae weak; 10) hypocone region of upper molars expanded (expanded talon) with a strong postprotocingulum; 11) notch between protoconid and metaconid on lower molars shallow to absent.

Discussion.—Paromomyidae are here viewed as members of the superfamily Plesiadapoidea based on the configuration of the upper incisors. Plesiadapoids can be differentiated from microsyopoids by the presence of tricuspid upper incisors in the former superfamily. Microsyopoids are characterized by having either bicuspid or single cusped upper incisors (particularly I^1). Upper incisors remain unknown in *Paromomys*, but are relatively well known in *Phenacolemur* where they are distinctly tricuspid. Further confirmation for *Paromomys* is needed to solidify this superfamily assignment, however this trait appears to best link paromomyids with plesiadapoids.

Paromomyinae, new subfamily

Included Genera.—Paromomys.

Emended Diagnosis.—Paromomyines differ from phenacolemurines by the retention of a number of primitive characteristics including the following: 1) 2–1–3–3 lower dental formula; 2) double-rooted P_2; 3) lower canine slightly larger than P_2 (where known); 4) P_3 double-rooted and large; 5) P^4 metacone weak to absent; 6) paraconid present on M_1; 7) M_3 talonid only slightly expanded by third lobe.

Discussion.—The features that unite the two species of *Paromomys* (*P. depressidens* and *P. maturus*) serve to indicate the relationship they share with the palaechthonid group. It is probable that both families were derived from a purgatorine-like ancestor and retention of a number of primitive character states is not surprising. However, these primitive retentions do not overshadow the derived features shared by paromomyines and phenacolemurines. The usefulness of separating *Paromomys* from its sister genera *Phenacolemur*, *Ignacius*, and *Elwynella* in different subfamilies may be questioned, however, I believe that this serves to emphasize the relationships between paromomyids and palaechthonids and to emphasize the presumed monophyletic origins of paromomyids. Further, phenacolemurids share a suite of features which are clearly derived in relation to their sister taxon *Paromomys*.

Paromomys Gidley, 1923

Paromomys Gidley, 1923, p. 3; Simpson, 1937a, p. 148., 1955, p. 420; Gazin, 1971, p. 29; Bown and Rose, 1976, p. 112; Krause, 1978, p. 1266; Rigby, 1980, p. 89.
cf. *Paromomys*, Tomida, 1981, p. 227.
cf. *Palaechthon* (in part), Tomida and Butler, 1980, p. 793.

Type Species.—Paromomys maturus

Included Species.—P. maturus, P. depressidens.

Diagnosis.—As for subfamily.

Distribution.—Torrejonian, middle Paleocene, of Montana, Wyoming, New Mexico, Utah, and Alberta.

Paromomys maturus Gidley, 1923

Paromomys maturus Gidley, 1923, p. 3, fig. 1–2, Pl. 1, fig. 2–3, Pl. 2, fig. 2–3; Simpson, 1937a, p. 148, fig. 30–31, Pl. 7, fig. 2,2a,3,3a, Pl. 8, fig. 2,2a,3,3a; 1955, p. 420, Pl. 34, fig. 1, Pl. 35, fig. 1; Bown and Rose, 1976, p. 112; Rigby, 1980, p. 89, Pl. 7, fig. 1–6.

Type.—USNM 9473, right mandible P_4-M_3.

Horizon and Locality.—Gidley Quarry, Torrejonian (Torrejonian Zone To_3), Fort Union Formation, Crazy Mountain Field, Montana.

Discussion.—Paromomys maturus is known only from two localities, the type locality Gidley Quarry and Swain Quarry in the Torrejonian Fort Union Formation, Carbon County, Wyoming (Rigby, 1980). Specimens from Swain Quarry confirm its dental formula as 2–1–3–3, as suggested by Szalay (1968). It differs from *P. depressidens* principally by being larger, although it also lacks the oblique postparacone and premetacone cristae which appear in *P. depressidens* (see Bown and Rose, 1976). It also differs from *P. depressidens* by having M_{1-2} trigonids less transverse than the talonids.

Paromomys depressidens Gidley, 1923

Paromomys depressidens Gidley, 1923, p. 4, fig. 3, Pl. 3, fig. 7; Simpson, 1937a, p. 154, fig. 32, Pl. 9, fig. 7; 1955, p. 420, Pl. 35, fig. 2; Bown and Rose, 1976, p. 112; Rigby, 1980, p. 8, Pl. 4, fig. 9–11, Pl. 6, fig. 1–4, Pl. 8, fig. 1–2.
P. cf. *depressidens*, Krause, 1978, p. 1266, fig. 9.
P. near *P. depressidens*, Gazin, 1971, p. 29, fig. 5a,5b.
cf. *Paromomys* sp., Tomida, 1981, p. 227, Pl. 10.1, fig. 1.
cf. *Palaechthon* sp. (in part), Tomida and Butler, 1980, p. 793, Pl. 2, fig. 3.

Type.—USNM 9546, right maxilla with P^4-M^3.

Horizon and Locality.—The type sample is from Gidley Quarry, Torrejonian, Fort Union Formation, Crazy Mountain Field, Montana. Other specimens are known from Rock Bench Quarry, Torrejonian, Fort Union Formation, Bighorn Basin, Wyoming; Swain Quarry, Torrejonian, Fort Union Formation, Carbon County, Wyoming; Locality 77113, Upper Kimbeto Arroyo, early Torrejonian, New Mexico; Dragon Canyon, early Torrejonian, Utah; Shotgun Member, Fort Union Formation, early Tiffanian, Wind River Basin, Wyoming; and Cochrane Site 11, Porcupine Hills Formation, late Torrejonian, Alberta, Canada (see Rigby, 1980, Tomida, 1981, Tomida and Butler, 1980, Gazin, 1971, and Krause, 1978 for details of the latter five localities).

Discussion.—I have included the fragmentary remains from Alberta, New Mexico, and the Wind River Basin of Wyoming in this species. As Gazin (1971) and Krause (1978) point out, the samples from the Shotgun member of the Fort Union and those from Cochrane Site 11 appear to be slightly more progressive than the type sample from

Gidley Quarry. The samples tend to be slightly smaller, have a better developed metacone on P^4, even more strongly anteriorly inclined molar trigonids, and have M_3 talonids less transversely restricted than in *P. depressidens*. All of these characteristics foreshadow developments in *Ignacius* and *Phenacolemur*. Based on biostratigraphic evidence, these two samples are probably later in time than is the type sample from Gidley Quarry. The Shotgun sample is probably earliest Tiffanian in age (see Gingerich, 1976, and below). Rigby (1980) notes the resemblance of *P. depressidens* to early *Phenacolemur* and suggests the possibility that *P. depressidens* may ultimately be shown to belong to a genus distinct from *Paromomys*. Until sampling improves this speculation will remain unsubstantiated.

The single tooth from the Kimbeto Arroyo in the San Juan Basin, New Mexico represents a paromomyid. Biostratigraphic and paleomagnetic information place the San Juan Basin "Dragonian" fauna (which includes this *Paromomys* specimen) near the Puercan-Torrejonian (early Paleocene-middle Paleocene) transition (Tomida, 1981). The tooth is a left lower molar interpreted by Tomida (1981) as an M_2. The paraconid is lingually placed and is appressed to the metaconid; however, a distinct paraconid cusp is still present. The talonid is broad and shallow but does not appear as broad relative to the trigonid as is the case for *P. maturus*. It is slightly larger than expected for *P. depressidens*, but smaller than *P. maturus*. Its assignment to *P. depressidens* remains tentative pending a more substantial sample. A similar specimen (UALP 10392), described by Tomida and Butler (1980) from Dragon Canyon, can also be tentatively assigned to this species.

The specimens from Swain Quarry (Rigby, 1980) and Rock Bench Quarry (12 specimens in the Princeton collection, see Rose, 1981a) are virtually indistinguishable from the type sample and add little to our understanding of this species. One additional specimen from Rock Bench Quarry (UM 76853), a left mandible with M_2, also represents *Paromomys depressidens*.

Phenacolemurinae (Simpson, 1955)

Type Genus.—Phenacolemur.

Included Genera.—Phenacolemur, Ignacius, Elwynella.

Distribution.—Late Torrejonian through Uintan of North American western interior; also Sparnacian of France (for *Phenacolemur*).

Emended Diagnosis.—Phenacolemurines are characterized as follows: 1) lower dental formula of 1–0-(1–2)-3; 2) lower canine and P_2 absent; 3) P_3 small and single or double rooted or absent; 4) P_4 premolariform, often enlarged; 5) P^4 metacone well developed; 6) M_1 with incipient to absent paraconid; 7) $M_{2\text{-}3}$ with paraconid absent; 8) M_3 hypoconulid doubled and greatly expanded into third lobe.

Discussion.—The features that unite phenacolemurines are clearly derived in relation to their sister taxon *Paromomys*. The earliest known representatives of phenacolemurines (*Ignacius fremontensis* and *Ignacius frugivorus*) have already lost the canine and P_2, and some specimens of *I. frugivorus* have also lost P_3 (Bown and Rose, 1976). The premolariform P_4 becomes enlarged in species of *Phenacolemur* to the point where it becomes the dominant tooth in the cheek tooth series. In *Ignacius* the P_4 remains relatively small. The upper P^4 develops a strong metacone and becomes squared off and semi-molariform. The upper molars of *Ignacius* and especially *Phenacolemur* expand the postero-lingual (hypocone) lobe and strengthen the postprotocingulum relative to the condition exhibited in *Paromomys*. In conjunction with this the paracristid becomes broad and transverse.

Elwynella is a poorly known genus (only the type mandible and two isolated teeth are known) from the Bridgerian Eocene of Wyoming (see Rose and Bown, 1982). It is peculiar in retaining a small, single-rooted P_3 and has an I_1 which is more lanceolate in appearance than is typical of the family. Paraconids are completely lacking on all molars (except USGS 2354 where M_1 has a small paraconid) and the paracristids are rather arcuate (Rose and Bown, 1982).

Together with paromomyines, phenacolemurines form a very closely related, probably monophyletic group. The separation of Paromomyidae from other palaechthonids seems justified if classification is to represent taxonomic affinities.

Palaechthonidae, new family

Type Genus.—Palaechthon.

Emended Diagnosis.—Palaechthonids can be characterized as follows: 1) I_1 procumbent, semilanceolate; 2) P_2 single-rooted; 3) molar mesoconids variably present, often strong; 4) paraconids on molars present, but may be weak on $M_{2\text{-}3}$; 5) $M^{1\text{-}3}$ conules present to strong; 6) $M_{1\text{-}3}$ protoconid-metaconid notch present and usually deep; 7) molar trigonids anteriorly inclined; 8) P_4 semimolariform.

Included Subfamilies.—Palaechthoninae, Plesiolestinae.

Age and Distribution.—Torrejonian and Tiffanian of Wyoming, Montana, Utah, Colorado, and New Mexico.

Discussion.—Palaechthonids can be distinguished from other Paleocene plesiadapiform families (except purgatoriids) quite easily. Palaechthonids differ from paromomyids by having a semi-lanceolate I_1, a single rooted P_2, strong upper molar conules and paraconids on all lower molars. Palaechthonids differ from plesiadapids by having a less robust I_1 (which is semilanceolate), by having semimolariform P_4, by lacking a protocone on P^3, and by having less bulbous, more acute cusps. They differ from carpolestids by lacking the plagiaulacoid P_4 development, by lacking cuspate $P^{3\text{-}4}$, and by having a more robust I_1. Palaechthonids differ from picrodontids by lacking the curious blade-like M_1 of the latter family.

Szalay and Delson (1979) characterize Paromomyini (including both paromomyids and palaechthonids in my interpretation) as having a reduced protocone on P^3, a reduced canine and an enlarged incisor. Krishtalka and Schwartz (1978) characterize Paromomyidae (again paromomyids and palaechthonids of this study) similarly as having a reduced protocone on P^4 (P^3 based on conventional homology), a less robust lower canine (I_1 based on conventional homology), and anteriorly inclined molar trigonids.

The loss or reduction of a protocone on P^3 is presumably a derived character shared by this group (according to both Szalay and Delson, 1979 and Krishtalka and Schwartz, 1978). However, P^3 remains unknown (or, at least, undescribed) in *Purgatorius*, and while many Cretaceous eutherians had a distinct protocone on P^3, not all did (for example, *Protungulatum* had a very small protocone, really just a basal, lingual cuspule). Given these qualifications, I do not believe that the polarity of this character has been established with certainty. A reduced canine may be a derived character for this group, however relative canine size is variable within palaechthonids (as defined in this paper) and canine reduction is not restricted to paromomyids and palaechthonids, as it is characteristic also of *Pronothodectes*, a plesiadapid. Krishtalka and Schwartz (1978) claim a less robust lower canine (I_1) as characteristic of Paromomyidae (in their sense). It is difficult to reconcile this with Szalay and Delson's (1979) characterization of an enlarged I_1 for Paromomyini. Presumably, Krishtalka and Schwartz were referring to the relatively less robust nature of I_1 in paromomyids and palaechthonids compared to plesiadapids. However, this does not clearly distinguish paromomyids and palaechthonids from carpolestids, as this family also has a relatively gracile I_1 in comparison with plesiadapids.

Bown and Gingerich (1973) and Bown and Rose (1976) discuss the possibilities (as does Gingerich, 1976; see also Van Valen, 1969) of a close relationship between Eocene Microsyopidae and Paleocene palaechthonids, including both in Microsyopidae. Szalay and Delson (1979) question this allocation. I prefer to separate the two groups on the familial level, but to retain them both within the same superfamily Microsyopoidea. The relationships between Paleocene palaechthonids and Eocene microsyopids will be more fully discussed in Chapter IV.

Palaechthoninae, new subfamily

Type Genus.—*Palaechthon.*

Included Genera.—*Palaechthon*, *Palenochtha*, and *Premnoides* (n.g.).

Age and Distribution.—Torrejonian (perhaps earliest Tiffanian, as well) of Wyoming, New Mexico, and Montana.

Emended Diagnosis.—Palaechthonids with the following characteristics: 1) canine smaller or equal in size to P_2; 2) P_4 metaconid absent to small; 3) P_4 with incipient to small entoconid; 4) hypoconulid on molars small and centrally placed (or slightly lingually placed); 5) hypoconulid notch weak; 6) preprotocristae distinct, postprotocristae weak and steeply angled; 7) preparaconule cristae usually continuous with precingulum (often not in *Palenochtha*); 8) postprotocingulum relatively weak.

Discussion.—The characters listed above seem to unite *Palaechthon*, *Palenochtha*, and *Premnoides*, although *Palenochtha* deviates from this diagnosis somewhat, away from the other two genera, but also away from plesiolestines. *Palenochtha*'s relationship to later Paleocene taxa, as well as Eocene taxa, will be discussed in Chapter V.

Palaechthon, *Palenochtha*, and *Premnoides* all share a canine that is either smaller or equal in size to P_2. The molarization of P_4 is less complete compared to plesiolestines (although some *Palaechthon* specimens have a fairly distinct metaconid), particularly in talonid structure, as the entoconid remains indistinct and small in nearly all specimens and the basin is less distinct and elevated than in plesiolestines. Hypoconulids remain small (as in *Purgatorius*) and the hypoconulid notch (a notch formed by the hypoconulid and the hypoconid) is weak (or often absent in *Palenochtha*). The hypoconulid is centrally or slightly lingually placed on the postcristid (contra Bown and Rose, 1976). The relatively weak and steeply angled postprotocrista is distinct in *Palaechthon*, less so in *Palenochtha* (but still present) and unknown in *Premnoides*. Postprotocingula are relatively weak, but certainly derived compared to *Purgatorius* (see Kielan-Jaworowska, Bown, and Lillegraven, 1979). Postprotocingulae in plesiolestines (where known) are more distinct.

Palaechthon Gidley, 1923

Palaechthon Gidley, 1923, p. 6; Simpson, 1937, p. 156; 1955, p. 19; Gazin, 1971, p. 26; Krause, 1978, p. 1263; Wood, Conroy, and Lucas, 1979, p. 3.

Palaechthon (in part), Szalay and Delson, 1979, p. 44; Kay and Cartmill, 1977, p. 24; Rigby, 1980, p 95; Gingerich, Houde, and Krause, 1983, p. 964; Tsentas, 1981, p. 272; Conroy, 1981, p. 166.

Type Species.—*Palaechthon alticuspis.*

Included Species.—*P. alticuspis*, *P. woodi.*

Age and Distribution.—Torrejonian and earliest Tiffanian, of Wyoming and Montana.

Emended Diagnosis.—*Palaechthon* differs from *Palenochtha* generally by being larger (although *P. woodi* is just slightly larger), by having more antero-posteriorly compressed molar trigonids, especially on $M_{2\text{-}3}$, by having a more molariform lower fourth premolar (with a better developed talonid basin), by lacking a distinct and separate metacone on P^4, by having more distinct and separate upper molar conules, by having upper molars that are less antero-posteriorly compressed lingually, by lacking a buccal cingulid on lower molars, and by having less elevated molar trigonids. Differs principally from *Premnoides* by retaining an I_2.

Discussion.—*Palaechthon* was one of Gidley's (1923) three original Paleocene genera. Its relationships with other Paleocene genera have been much discussed in the past. It has recently been viewed as congeneric with *Plesiolestes* and *Torrejonia* (Rigby, 1980), distinct from *Torrejonia* but congeneric with *Plesiolestes* (Gingerich, Houde, and Krause, 1983), and as distinct from both genera (Szalay and Delson, 1979, who synonymize *Plesiolestes* and *Torrejonia*). The difficulties arise from the relatively small number of specimens and their rather wide-spread geographic distribution. Based on a thorough study of the Rock Bench Quarry type sample of *Plesiolestes*, I believe that *Palaechthon* can be distinguished from that taxon. *Torrejonia*, known only by a very few specimens, is also distinct from *Palaechthon*, as I shall discuss below.

Palaechthon alticuspis Gidley, 1923

Palaechthon alticuspis Gidley, 1923, p. 6, Pl. 1, fig. 1; Simpson, 1937a, p. 156, Pl. 34, fig. 2, Pl. 35, fig. 3; 1955, p. 419, Pl. 7, fig. 1, Pl. 9, fig. 5,6; Kay and Cartmill, 1977, p. 24, fig. 2; Szalay and Delson, 1979, p. 44, fig. 14a,b,d.

Palaechthon, near *P. alticuspis*, Gazin, 1971, p. 26.

Holotype.—USNM 9532, right mandible with P_2-M_2.

Horizon and Locality.—Known from the type locality, Gidley Quarry, Fort Union Formation, Crazy Mountain Field, Sweetgrass County, Montana, and from Shotgun Local Fauna, Wind River Basin, Wyoming.

Emended Diagnosis.—Differs from *Palaechthon woodi* by being significantly larger, by having a relatively more molarized P_4 with a better developed talonid basin with a small entoconid, by having a better developed paraconid on P_4, by having $M_{2\text{-}3}$ with slightly better differentiated paraconids, and by having a relatively deeper protoconid-metaconid notch.

Discussion.—Palaechthon alticuspis, as here defined, is known only from Montana at Gidley Quarry, and possibly from Keefer Hill. It is sufficiently distinct from *P. woodi* to maintain two species in this genus. It is significantly larger, based on lower first molar dimensions, than *P. woodi* (Table 1 gives summary statistics for *Palaechthon alticuspis* and *Palaechthon woodi*).

Palaechthon woodi

Palaechthon woodi Gazin, 1971, p. 23, fig. 4a; Wood, Conroy, and Lucas, 1979, p. 3, fig. 1; Conroy, 1981, p. 166, fig. 7.1–7.4, 7.6; Tsentas, 1981, p. 272; Kay and Cartmill, 1977, p. 24, fig. 2; Szalay and Delson, 1979, p. 44.

Cf. *"Palaechthon" woodi*, Gingerich, Houde, and Krause, 1983, p. 964, fig. 2g.

Holotype.—MCZ 18740, left mandible with P_4-M_2.

Horizon and Locality.—The type is from the Shotgun Local Fauna, Shotgun Member of the Fort Union Formation, Wind River Basin, Wyoming. Additional specimens are known from the Torreon Wash, San Juan Basin, New Mexico, and possibly from the Bangtail Locality, Fort Union Formation, Montana.

Table 1. Summary Statistics for *Palaechthon alticuspis* and *Palaechthon woodi*. Abbreviations: N = sample size; OR = observed range; $\bar{X}$ = mean; S = standard deviation; V = coefficient of variation; L = length; W = width. All measurements in millimeters (mm).

Tooth Position	Parameter	N	OR	$\bar{X}$	S	V
Palaechthon alticuspis						
M_1	L	10	1.9–2.1	2.03	0.08	3.8
	W	9	1.5–1.7	1.57	0.07	4.2
M_2	L	12	1.9–2.2	2.07	0.09	4.1
	W	11	1.5–1.8	1.68	0.08	5.0
Palaechthon woodi						
P_4	L	1		1.6		
	W	1		1.1		
M_1	L	1		1.8		
	W	1		1.3		
M_2	L	1		1.9		
	W	1		1.4		

Discussion.—This species of *Palaechthon* remains poorly known. The only relatively complete specimen is the type, the specimens from Torreon Wash and Bangtail being isolated teeth. Those from Torreon Wash are all lower molars and agree in size and overall morphology with the type. The only specimen from Bangtail is an upper molar (Gingerich, Houde, and Krause, 1983) that agrees in size with *P. woodi* and is morphologically similar to other palaechthonines. Until associated uppers and lowers are discovered, its assignment to *P. woodi* will remain tentative.

As Gingerich, Houde, and Krause (1983) point out, *P. woodi* differs from the genotype *P. alticuspis* in morphological detail and may represent a new genus.

Premnoides, new genus

Type Species.—Premnoides douglassi

Etymology.—Premnon, Gr., base of tree, stem; oides, like, resembling, from Gr. eides, in reference to this genus's resemblance to both plesiolestines and palaechthonids, as well as *Pronothodectes* and *Paromomys*, and thus its resemblances to the presumed plesiadapiform stem group.

Diagnosis.—Differs from *Palaechthon* by the loss of one anterior tooth (presumably I_2), by having more strongly antero-posteriorly compressed molar trigonids (especially $M_{2\text{-}3}$), by having more squared molar trigonids with lingually placed paraconids, by lacking any trace of a paraconid on P_4, and by having small but distinct mesoconids on $M_{1\text{-}3}$. Differs from *Palenochtha* by having less distinct paraconids on $M_{2\text{-}3}$, by having a small but distinct mesoconid on lower molars, by having molar trigonids much more strongly antero-posteriorly compressed, by having a relatively shallow protoconid-metaconid notch, by lacking a paraconid on P_4, and by lacking a distinct buccal cingulid on lower molars.

Discussion.—Rose (1981a) was the first to note the distinctive nature of this genus, although he chose not to formally recognize a new genus at that time. He noted that this genus was distinctive in sharing features with plesiadapids, microsyopids (here viewed as palaechthonids), and paromomyids. Rose (1981a) noted the squared off trigonids with lingually placed paraconids on the lower molars reminiscent of *Paromomys*, the development of a small mesoconid that many palaechthonids also share, and the slightly rugose enamel similar to some plesiadapids.

Premnoides bears rather close resemblances with many plesiolestines and palaechthonines. In over-all characteristics, *Premnoides* most closely resembles *Palaechthon*. The major distinguishing features of *Premnoides* include a more premolariform P_4, with an undeveloped talonid basin (no entoconid) and the lack of a paraconid or metaconid on the P_4 trigonid. The molars of *Premnoides* have less distinct and more lingually placed paraconids and less transverse talonids. *Premnoides* resembles *Paromomys* in its squared off molar trigonids with weak paraconids, however *Premnoides* does retain small but distinct paraconids on M_{2-3} and its talonid basins are not bucco-lingually inflated as in *Paromomys*. The molar trigonids of *Premnoides* are not strongly inclined anteriorly as in *Paromomys*, but are more upright, even less anteriorly inclined than in *Palaechthon*. The simplified premolars and the relatively upright molar trigonids are similar to *Palenochtha*, but *Premnoides* lacks the distinct molar paraconids of *Palenochtha* and does not possess a buccal cingulid on its molars as does *Palenochtha* (although this character appears more variable than previously thought in *Palenochtha*).

Premnoides is less similar in over-all characteristics to plesiolestines than to palaechthonines, however it does share some characters with the former group. *Premnoides* has an incipient mesoconid which is characteristic of *Plesiolestes*, although some *Palaechthon* specimens also share this character. *Premnoides* has a rather distinct hypoconulid and may have a small but distinct hypoconulid notch (especially on M_2) which is characteristic of *Plesiolestes*. *Premnoides* also has a bilobed extension on its M_3 talonid which is characteristic of *Plesiolestes*. *Premnoides* differs from *Plesiolestes* by lacking a molariform P_4 and by having less distinct molar paraconids and more antero-posteriorly compressed molar trigonids. *Premnoides* resembles *Torrejonia* in lacking a paraconid and metaconid on P_4, but *Torrejonia* has a much better developed P_4 talonid, with distinct hypoconid and entoconid cusps.

Premnoides douglassi, new species
Figure 4

Plesiadapiform, Rose, 1981a, p. 146.

Holotype.—PU 14802, right mandible with P_3-M_1.

Type Locality.—Rock Bench Quarry, NW1/4, NE1/4, Section 36, T57N, R99W, Park County, Wyoming.

Age and Distribution.—Torrejonian, middle Paleocene, Fort Union Formation. At present only known from type locality.

Referred Specimens.—Type and PU 19794.

Etymology.—Named for Earl Douglass, collector of the first plesiadapiform found in North America (*Picrodus*).

Diagnosis.—Sole known species of genus. See generic diagnosis.

Description.—The type specimen of *P. douglassi* preserves the alveolus of P_2, P_3-M_1, and an alveolus for M_2. Beneath the P_2 alveolus and extending posteriorly, at least, to the base of P_3, is the root of the central incisor. The root of I_1 is bucco-lingually compressed and is oval in cross-section. Just buccal to the root of I_1 and anterior to the P_2 alveolus is a small depression which may have been the base of the alveolus for a small canine. There is no evidence of an I_2 root, so *P. douglassi* had a dental formula of 1–1–3–3. P_2 was single rooted and smaller than P_3. P_3 is double rooted and has a single cusped trigonid. There is a tiny raised edge of enamel running anteriorly from the trigonid cusp (protoconid) in the position of the paracristid. P_3 has a small talonid cusp (hypoconid?) whose lingual surface slopes anteriorly and ventrally to join a tiny lingual shelf. P_4 is very similar to P_3, but the talonid cusp is expanded and the lingual sloping surface is more developed, but the lingual shelf is relatively the same size. The P_4 trigonid has no paraconid or metaconid, however there is a tiny bulge of enamel on the metaconid surface of the posterior flank of the protoconid.

The first lower molar has a protoconid and metaconid of equal height, with a shallow notch separating the two cusps. The metaconid is slightly posterior to the protoconid, while both cusps are rounded off and more bulbous than is seen in *Palenochtha*. The paraconid is separated from the metaconid but is small and rather low on the anterior flank of the metaconid, and is lingually placed. The paracristid runs bucco-lingually and is longer (relatively) than is typical of *Palaechthon*. The talonid basin is rather narrow transversely and has distinct, but low and rounded, hypoconids and entoconids. The hypoconulid is small and centered on the postcristid. There is only a slight buccal cingulid developed that wraps anteriorly around the base of the protoconid. There is no lingual cingulum below the hypoflexid. PU 19794 preserves the morphology of M_{1-3}. M_1 is similar to that of the type, differing only in having a slightly better defined hypoconulid, appearing as a separate talonid segment as in *Plesiolestes*.

M_2 is similar to M_1 except that the paraconid is less well defined (although present). The M_2 trigonid is more antero-

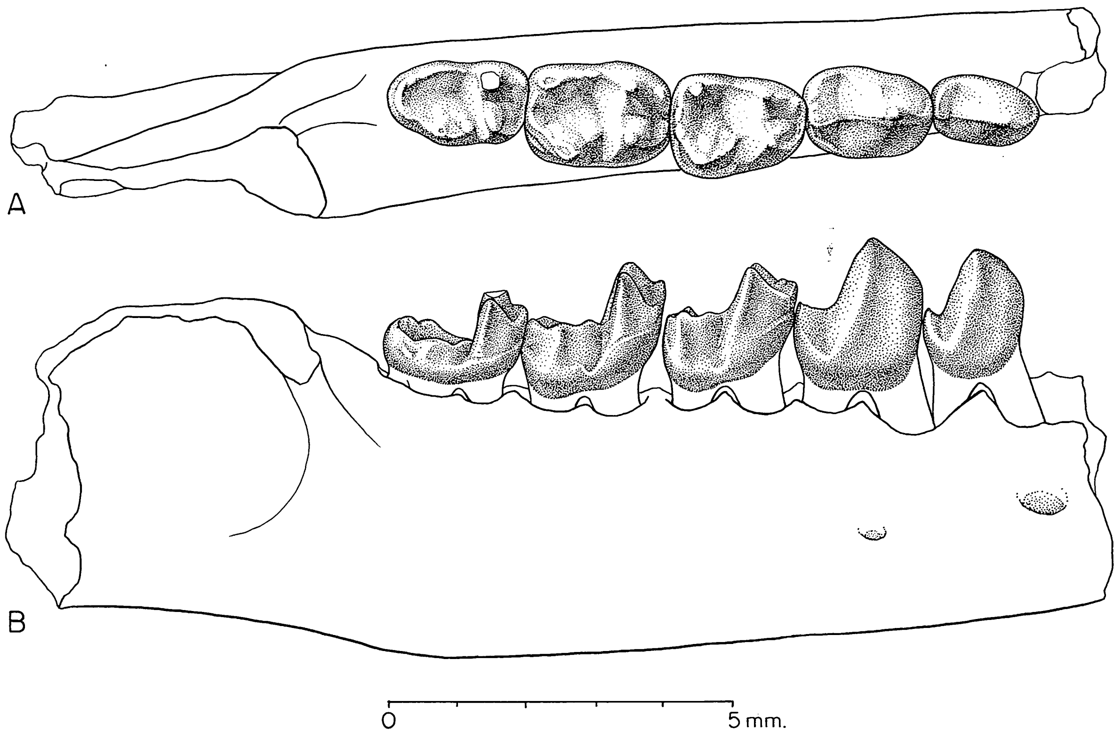

Figure 4. *Premnoides douglassi*, new genus and species. A, occlusal view of composite (YPM-PU 14802, holotype, and YPM-PU 19794), showing P_3-M_3. B, same in lateral view.

posteriorly compressed than in M_1 and the paracristid is relatively longer bucco-lingually. The talonid is narrow, as in M_1, but the hypoconulid is better developed as a separate talonid segment and there is a small but distinct hypoconulid notch developed.

M_3 is smaller transversely than either M_1 or M_2, but is nearly as large antero-posteriorly. The trigonid cusp configuration is as in M_2. The talonid is narrow transversely, but is extended posteriorly. This talonid extension is formed by a bicuspid development of the hypoconulid segment, similar to *Plesiolestes*, but differing from *Palaechthon* and *Palenochtha*.

The molar trigonids of all three molars are only slightly inclined anteriorly, less-so than in *Palaechthon* but similar to *Palenochtha*. The mandible is rather shallow, deepening slightly below M_{2-3}. The masseteric fossa is relatively deep. There are two mental foramina preserved on the type, one below the anterior root of P_3 and the other just posterior to the anterior root of P_4. Table 2 present the measurements of *Premnoides douglassi*.

Discussion.—The evidence about the anterior dentition provided by the type specimen is rather equivocal; however, it is suggestive of palaechthonids. The base of the canine root is rather small, suggesting a small canine, which would ally this genus with palaechthonids. The canine root begins beneath the root of P_2, indicating that these teeth were probably crowded together, and that the anterior portion of the jaw was relatively shorter than in *Palaechthon*, although there is some evidence to suggest a similar condition in *Palenochtha* (see Simpson, 1937a; Szalay and Delson, 1979; but also see below).

Table 2. Measurements of *Premnoides douglassi*
Abbreviations as in Table 1. All measurements in mm.

Tooth Position	Parameter	N	OR	$\bar{X}$
P_3	L	1		1.5
	W	1		1.0
P_4	L	1		2.0
	W	1		1.2
M_1	L	2	2.0–2.1	2.05
	W	2	1.3–1.4	1.35
M_2	L	1		2.1
	W	1		1.5
M_3	L	1		2.1
	W	1		1.5

The definitive evidence for the loss of I_2 is lacking. However there is no trace of an I_2 root, which suggests that this tooth was either lost or very small. If the interpretation of the lower dental formula as 1–1–3–3 is correct, *Premnoi-*

des is even more clearly distinct from *Palaechthon* and *Plesiolestes* (as well as *Paromomys*). This dental formula is shared with *Palenochtha* (although *Palenochtha weissae* has a dental formula of 1–1–4–3, according to Rigby, 1980). However the molar morphologies of these two genera are clearly different and warrant generic separation.

Premnoides presents an interesting mosaic of primitive, generalized features combined with some derived features (particularly if the dental formula is correct as interpreted). Its resemblances with both palaechthonids and paromomyids is evidence to suggest the plesiadapoids and microsyopoids may have been derived from a common ancestor and supports a monophyletic origin for Plesiadapiformes. However, the relationships between microsyopoids and plesiadapoids still remains unclear. *Pronothodectes* (the first plesiadapid) differs in a number of ways from any microsyopoid (as does *Elphidotarsius*, the first carpolestid). Paromomyids are more similar to microsyopoids, but this may only reflect shared, primitive characteristics.

Palenochtha Simpson, 1935

Palenochtha Simpson, 1935, p. 231; 1937a, p. 159; Gazin, 1971, p. 23; Szalay and Delson, 1979, p. 49; Rigby, 1980, p. 93.

Palaechthon (in part), Gidley, 1923, p. 7.

Type Species.—*Palenochtha minor*.

Included Species.—*Palenochtha minor*, *Palenochtha weissae*.

Emended Diagnosis.—Differs from *Palaechthon* and *Premnoides* by being significantly smaller, by having distinct and separate paraconids on lower molars, by having more open, less antero-posteriorly compressed molar trigonids, and by having a distinct buccal cingulid on lower molars. Further differs from *Palaechthon* by the loss of I_2 (see *P. weissae* discussion below), by having a very tiny to absent paraconid on P_4, by having a weakly developed talonid basin on P_4 (although this appears variable, see *P. minor* discussion below), and by having a distinct and separate metacone on P^4. Further differs from *Premnoides* by lacking a mesoconid and by having a deep protoconid-metaconid notch.

Palenochtha minor (Gidley, 1923)

Palenochtha minor (Simpson, 1935), p. 231; 1937a, p. 159, fig. 33, Pl. 10, fig. 1; Szalay and Delson, 1979, p. 49, fig. 17a-f.

Palenochtha, cf. *minor*, Gazin, 1971, p. 23; Rigby, 1980, p. 93, Pl. 5, fig. 15–17.

Palaechthon minor Gidley, 1923, p. 7, Fig. 4, Pl. 4, fig. 1.

Holotype.—USNM 9639, right mandible with P_4-M_3 and alveoli for C_1, $P_{2\text{-}3}$.

Age and Distribution.—Type sample is from Gidley Quarry, Torrejonian, Crazy Mountain Field, Montana. Additional specimens are known from Rock Bench Quarry, Torrejonian, Park County, Wyoming; Swain Quarry, Torrejonian, Carbon County, Wyoming; and from Shotgun Butte, early Tiffanian, Freemont County, Wyoming.

Diagnosis.—Differs from *P. weissae* in lacking a P_1.

Discussion.—The Rock Bench Quarry sample of *Palenochtha* has never been adequately described. While this sample represents *P. minor*, it does show some minor variations from the type sample. One specimen (PU 14786) preserves most of the central incisor, as well as, P_4-M_3, and the ascending ramus (see Figure 5), while PU 19461 preserves $M_{1\text{-}3}$ and all of the anterior alveoli.

The lower central incisor preserved in PU 14786 is somewhat broken and the tip is lost, although the over-all morphology has been preserved. It has a rather stout, laterally compressed root that extends posteriorly to the anterior root of P_3. It is much more procumbent than the reconstruction presented by Szalay and Delson (1979, p. 50). The crown is laterally compressed and is semilanceolate in medial outline. There is a distinct ridge of enamel along the dorsal margin and a smaller enamel ridge running anteriorly, parallel and medial to the dorsal ridge. Below this medial ridge, the enamel is smooth and gently rounded to the ventral margin. It is similar, morphologically, to *Navajovius* (see Chapter IV) but is less lanceolate and less dorsally flared than this genus (or later microsyopids).

Immediately posterior to the I_1 there is a fairly large, vertically oriented alveolus. Posterior to this is another single rooted alveolus of approximately the same size or slightly smaller than its anterior neighbor. Szalay and Delson (1979) interpret these two alveoli as representing I_2 and the lower canine. Posterior to these alveoli are two alveoli that represent the double rooted P_3, which is followed by a double rooted P_4. In Szalay and Delson's (1979) interpretation, the lower dental formula for *P. minor* would be 2–1–2–3. Rigby (1980) describes a new species of *Palenochtha*, *P. weissae* (see below), which differs from *P. minor* by the retention of an additional anterior tooth. He states that AMNH 100356 (the holotype of this species) preserves, at least, five alveoli anterior to P_4. There is a large, vertical alveolus anteriorly, followed by a small, single rooted alveolus, followed by a bilobate alveolus and two other alveoli representing the double rooted P_3. The large, vertical anterior alveolus is presumably for the lower canine, although this is not explicitly stated by Rigby. Following this is the small, circular alveolus, interpreted by Rigby to represent that of P_1. The bilobate alveolus represents P_2. The dental formula for *P. weissae* could conceivably be either of the following: 2–1–3–3 (if the vertical anterior root is viewed as an I_2, as Szalay and Delson would interpret it); or 1–1–4–3 (viewing the anterior, vertical alveolus as a canine). Both of these suggested dental formulas assume that anterior to the vertically implanted tooth of *P. weissae* there is at least one additional tooth, representing the I_1.

The fact that the anterior alveoli in both species of *Pale-*

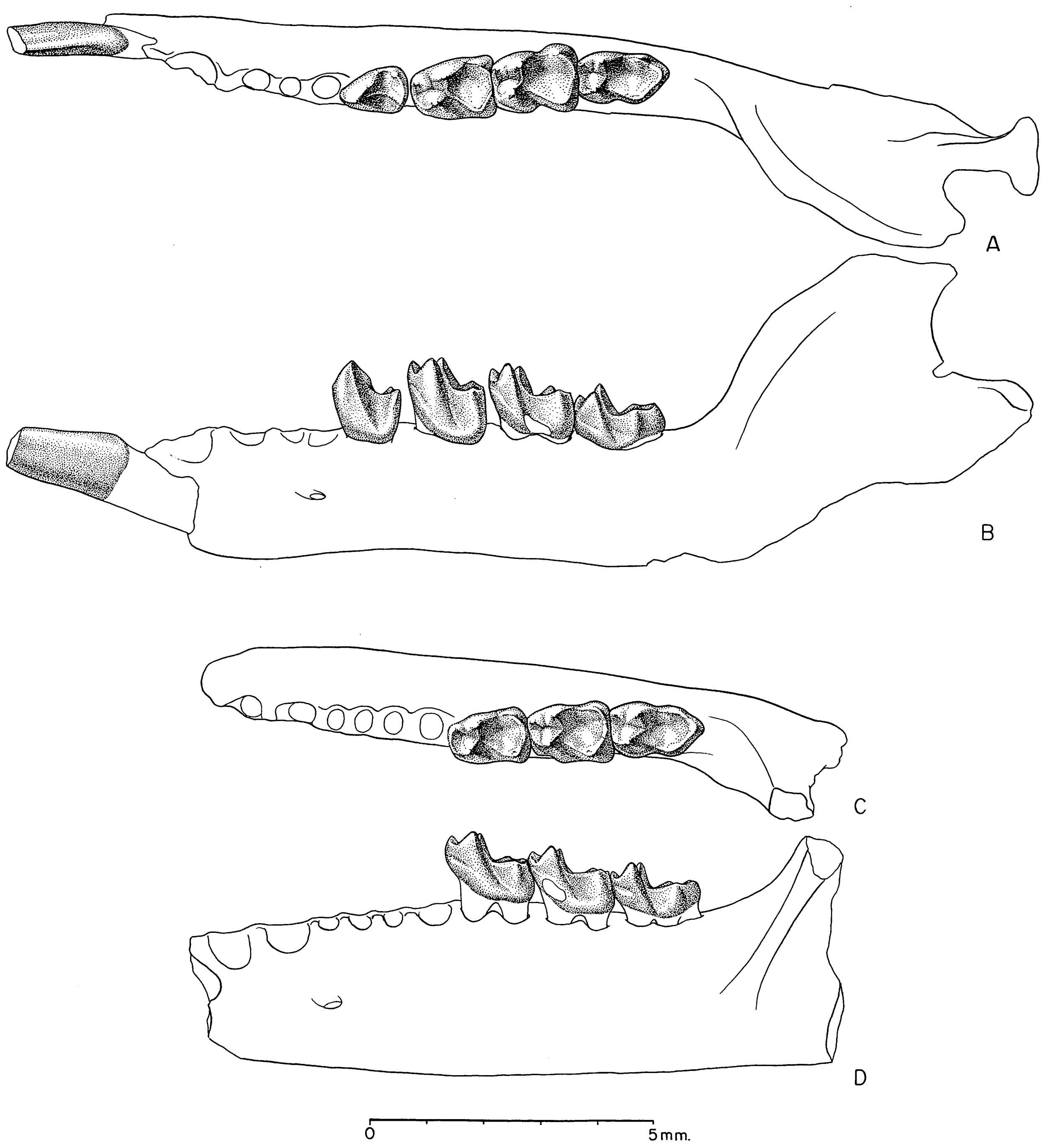

Figure 5. *Palenochtha minor* from Rock Bench Quarry. A, YPM-PU 14786, left mandible with I_1, P_4-M_3, in occlusal view. B, same in lateral view. C, YPM-PU 19461, left mandible with M_{1-3}, in occlusal view. D, same in lateral view.

nochtha are vertically implanted suggests that the tooth that is represented by these alveoli is probably a canine and indicates that I_2 is probably lost in both. The canine in *Palaechthon* is vertically implanted, while I_2 is oriented more anteriorly and somewhat lateral to the I_1. The anterior alveolus in *Palenochtha* is not only implanted vertically but also is positioned posteriorly to the I_1 (as in *Palaechthon*). This supports its interpretation as a canine. The dental formulae suggested here for *P. minor* and *P. weissae* are 1–1–3–3 and 1–1–4–3, respectively.

P_4 is preserved in PU 14786. It differs from *P. minor* from Gidley Quarry in being slightly larger, by having a slightly better developed paracristid, and by having a better developed talonid. The talonid is more basined and has a small but distinct entoconid cuspule.

The molars preserved in PU 14786 and PU 19461 are very similar morphologically to the type sample of *P. minor* from Gidley Quarry, but there are some minor differences. The Rock Bench sample has molars that are larger in both length and width, except that M_3 is shorter than the type sample from Gidley. The Rock Bench sample of molars have relatively broader and longer talonid basins with stronger entoconids. The paraconids (especially on $M_{2\text{-}3}$) are even more distinct than the Gidley specimens. The Rock Bench sample has slightly more anteriorly inclined trigonids and the M_3 talonid is less expanded than is typical of the *P. minor* type sample. These last two characters are similar to those shown in the Swain Quarry sample (Rigby, 1980).

The mandibles of Rock Bench Quarry *P. minor* are very slender and gracile, the typical condition for *Palenochtha*. The ascending ramus of PU 14786 is slightly broken and distorted, but it is apparent that the coronoid process was relatively high and the articular condyle rose above the level of the tooth row. The masseteric fossa appears to have been rather deep. There is one mental foramen preserved below the roots of P_3, as in *P. minor* from Gidley Quarry.

While I have referred these two Rock Bench Quarry specimens to *P. minor*, this assignment should be viewed as tentative, pending larger samples. These specimens are larger than is typical for *P. minor*, and they have some characteristics convergent with *Palaechthon*, such as the slightly greater anterior slope of the molar trigonids and the more molarized P_4. The differences exhibited by the Rock Bench specimens are not distinctive enough to warrant specific separation from *P. minor* at this time. However, when sampling improves, it may be possible to diagnose specific differences in these Rock Bench primates.

Palenochtha weissae Rigby, 1980

Palenochtha weissae Rigby, 1980, p. 94, Pl. 5, fig. 12–14.

Holotype.—AMNH 100356, mandible with P_4 and anterior alveoli.

Age and Distribution.—Torrejonian, middle Paleocene, Swain Quarry, Carbon County, Wyoming.

Diagnosis.—Differs from *P. minor* by retaining an additional anterior tooth, probably P_1 (see discussion above).

Discussion.—Rigby (1980) described this poorly known primate based on three fragmentary mandibles. Nothing further can be added to his description and discussion.

Palenochtha is not as advanced an early primate as suggested by Szalay and Delson (1979). Certain of its characteristics, such as relatively large incisors, relatively high and upright molar trigonids, and distinct lower molar paraconids can all be viewed as primitive, although the paraconid differs morphologically from that in *Purgatorius*. The large buccal cingulids on lower molars are a derived character, but its development is somewhat variable, ranging from small to well developed.

The simple, premolariform premolars are viewed by Szalay and Delson (1979) as secondarily derived as the result of mandibular shortening and changes in the relative positions of anterior teeth in the mandible. PU 14786 demonstrates that the mandible of *Palenochtha* was not significantly shortened relative to the condition in *Palaechthon*, as *Palenochtha* only shows the loss of one incisor. The presence of a P_1 in *P. weissae* also argues against interpreting *Palenochtha* as highly derived. I believe that it is just as plausible to view *Palenochtha* as retaining a number of primitive characteristics, with only a loss of I_2 and the development of a buccal cingulid on lower molars being viewed as synapomorphies, the latter possibly being an autapomorphous condition.

Small canine size is a characteristic of palaechthonines (see above). In Szalay and Delson's interpretation, *Palenochtha* has a reduced canine, while in my interpretation the canine remains relatively larger. Since the canine crown is unknown in *Palenochtha* and the crown of P_2 is only known in broken specimens, it is difficult to say, with any certainty, what the relative sizes are. It is possible, judging from the alveoli, that the canine was slightly larger than the P_2 in *Palenochtha* (or about the same size), which might suggest a closer relationship with plesiolestines (see below). However, plesiolestines (where known) have a canine that is significantly larger than P_2. *Palenochtha* also differs from *Plesiolestes* and resembles palaechthonines in its relatively simple premolars and its unexpanded (or only slightly expanded) M_3 talonid. It also shows a weak postprotocrista, as in other palaechthonines.

Palenochtha seems to share more features with palaechthonines than with plesiolestines and is included here with the former subfamily, although *Palenochtha* also has some unique features (particularly the buccal cingulid) which make its taxonomic assessment difficult. In many ways *Palenochtha* resembles later diminutive microsyopids. These relationships will be discussed in Chapter V.

Plesiolestinae, new subfamily

Type Genus.—*Plesiolestes*.

Included Genera.—*Plesiolestes*, *Torrejonia*.

Age and Distribution.—Torrejonian and Tiffanian, middle and late Paleocene of Wyoming, New Mexico, and Montana.

Emended Diagnosis.—Palaechthonids with the following characteristics: 1) lower canine larger to much larger than P_2 (where known); 2) P_4 talonid with a strong basin and normally distinct entoconid; 3) lower molar trigonids more antero-posteriorly compressed than in palaechthonines; 4) lower molar trigonids with smaller and lower paraconids; 5) hypoconulids small to very strong, shallow to very distinct hypoconulid notch; 6) hypoconulid centrally to lingually placed; 7) preprotocristae and postprotocristae strong and distinct; 8) preparaconule cristae normally not continuous with precingula; 9) postprotocingulum present to strong; 10) M_3 talonid with strong bilobed hypoconulid (except in *P. nacimienti*).

Discussion.—Plesiolestes and *Torrejonia* seem to be linked together by the above characteristics, although some of them are not yet known in *Torrejonia*. Plesiolestines all tend to be larger than palaechthonines. Canines are larger than P_2 (probably due to a reduction in P_2 size, since a relatively large canine seems to be primitive for plesiadapiforms, as in *Purgatorius*) in all specimens where these teeth or alveoli are known. Relatively large canine size in *Purgatorius* indicates the primitive nature of large canines (Clemens, 1974; Kielan-Jaworowska, Bown, and Lillegraven, 1979); however, judging from the alveoli, the P_2 was not much smaller than the canine. Palaechthonines retain the primitive condition of a relatively large canine and P_2, while plesiolestines are more derived with a reduced P_2.

Both *Plesiolestes* and *Torrejonia* have very strong P_4 talonid (although one specimen of *P. nacimienti* has a relatively weaker talonid basin, but the specimen is heavily worn). Both have bilobed, rather strongly developed, M_3 hypoconulids (although this feature is again less well developed in *P. nacimienti*). The molar trigonids tend to be slightly less anterio-posteriorly compressed with slightly more distinct paraconids than in palaechthonines and the hypoconulids tend to be stronger and often more lingually placed. The hypoconulid notch, especially in *Plesiolestes*, is well developed.

In the upper molars, the most distinctive characters are a strong postprotocrista, not weak and steeply angled as in palaechthonines, and a preparaconule crista that is normally distinct and separate from the precingulum. The latter characteristic is often present in *Palenochtha* as well, but *Palenochtha*, like other palaechthonines, lacks distinct postprotocristae. *Torrejonia* upper molars are not well known (see Gazin, 1968, 1971), but if the allocation of isolated uppers is correct, *Torrejonia* does show a distinct postprotocrista. The preparaconule crista of *Torrejonia* may not be as distinctly separated from the precingulum as it is in *Plesiolestes* (although it appears to be in *T. sirokyi*).

As a group, plesiolestines seem to be adding additional shearing surfaces to their molars and to P_4, which tend to be more flattened in appearance than is the case in palaechthonines. In addition, the cusps tend to be more rounded and bulbous and less acute in plesiolestines. Molar paraconids, while distinct, tend to be lower on the anterior surface of the trigonid. The presence of a distinct hypocone, or at least, a well developed postprotocingulum, indicates an increased element of paracristid-hypocone-hypocrista shearing. The larger size and better developed crushing surfaces indicates a shift from a presumed completely insectivorous dietary regime in palaechthonines, to a more diverse, omnivorous dietary regime in plesiolestines.

Plesiolestes Jepsen, 1930b

Plesiolestes Jepsen, 1930b, p. 505; Bown and Gingerich, 1973, p. 1; Bown and Rose, 1976, p. 135.

Plesiolestes (in part), Szalay, 1973, p. 83; Szalay and Delson, 1979, p. 47.

Palaechthon(in part), Wilson and Szalay, 1972, p. 5; Kay and Cartmill, 1977, p. 22; Rigby, 1980, p. 95; Conroy, 1981, p. 164; Taylor, 1981, p. 259; Tsentas, 1981, p. 272; Gingerich, Houde, and Krause, 1983, p. 964.

cf. *Palaechthon* (in part), Tomida and Butler, 1980, p. 793.

Paromomyid, Tomida and Butler, 1980, p. 794.

Talpohenach Kay and Cartmill, 1977, p. 45; Taylor, 1981, p. 259; Tsentas, 1981, p. 272.

Type Species.—Plesiolestes problematicus.

Included Species.—P. problematicus, P. nacimienti.

Age and Distribution.—Torrejonian and possibly earliest Tiffanian, middle and late Paleocene of New Mexico, Utah, Wyoming, and Montana.

Emended Diagnosis.—Differs from *Torrejonia* by the following characteristics: 1) by having a small to distinct metaconid on P_4; 2) by having an incipient to small paraconid on P_4; 3) by having less rounded, more acute cusps; 4) in being smaller.

Discussion.—It is apparent that *Plesiolestes* and *Torrejonia* are closely related. Szalay and Delson (1979) have synonymized them, noting particularly the resemblances between the species allocated to each genus. Part of the problem was Szalay's (1973) original allocation of the species *sirokyi* to *Plesiolestes*. *P. sirokyi* appears to me to be much more comfortably contained within *Torrejonia*, as that genus was originally described by Gazin (1968). Szalay (1973) included *sirokyi* in *Plesiolestes* because, "the molars and premolars are very similar in the total balance of their characters to *Plesiolestes problematicus*. . . . . . . No particular diagnostic features distinguish either the known premolars or molars from those of the generotype." This description overlooks the obvious resemblances of the premolars, particularly P_4, to *Torrejonia*. Both species lack distinct paraconids and metaconids on P_4, while the generotype, *Plesiolestes problematicus*, has both, often very distinct, and never lacks, at least, some development of each.

Plesiolestes problematicus Jepsen, 1930b
Figure 6

Plesiolestes problematicus Jepsen, 1930b, p. 505, Pl. 4, fig. 6,7; Bown and Gingerich, 1973, p. 1, fig. 1a,2a,3a; Szalay, 1973, p. 83, fig. 6–8; Bown and Rose, 1976, p. 135; Kay and Cartmill, 1977, p. 22, fig. 1; Szalay and Delson, 1979, p. 47, fig. 16a-g.

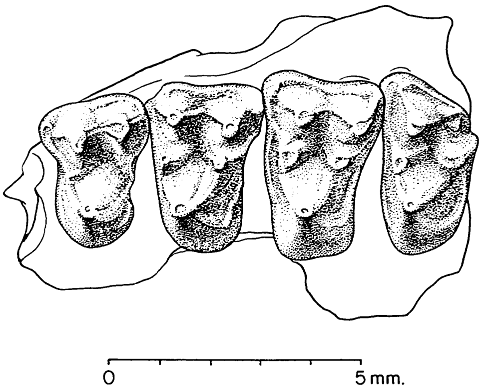

Figure 6. *Plesiolestes problematicus* from Rock Bench Quarry. YPM-PU 14304, left maxilla with P^4-M^3, in occlusal view.

Palaechthon problematicus, Rigby, 1980, p. 95; Gingerich, Houde, and Krause, 1983, p. 964, fig. 2f.

Holotype.—PU 13291, right mandible with P_3, M_{1-3}.

Type Locality.—Rock Bench Quarry, Fort Union Formation, Bighorn Basin, Wyoming.

Age and Distribution.—Torrejonian (middle Paleocene) and possibly earliest Tiffanian (late Paleocene) of Wyoming and Montana.

Emended Diagnosis.—*P. problematicus* differs from *P. nacimienti* by having a better developed talonid on both P_3 and P_4, by having a more distinct mesoconid on lower molars, by having a very strongly developed, bilobed hypoconulid on M_3, by having M_3 more expanded, less reduced, by having more distinct paraconids on lower molars, and by having weaker hypocones and precingula on upper molars.

Discussion.—The Rock Bench sample of *Plesiolestes problematicus* is quite large. Table 3 presents a summary of the dental measurements of this sample. *P. problematicus* is also known from Swain Quarry (see Table 4 for measurements), from the Tongue River Formation of the Medicine Rocks area in Montana (see Table 5 for measurements), and from Keefer Hill, Shotgun Butte in Wyoming (see Table 6 for measurements). Gingerich, Houde, and Krause (1983) also report its presence in the Bangtail fauna from Montana.

I cannot agree with Rigby (1980) nor with Simpson (1937), Gingerich (1976, 1980), or Gingerich, Houde, and Krause (1983) that *Palaechthon* and *Plesiolestes* are congeneric. *P. problematicus* is more advanced than is its sister species, *P. nacimienti*. The features distinctive of plesiolestines are well developed in *P. problematicus*, including a molariform P_4, distinct hypoconulid, and a strong hypoconulid notch on lower molars and a well developed, bilobed hypoconulid on M_3. The Rock Bench and Tongue River samples confirm that these characteristics are not

Table 3. Summary Statistics of *Plesiolestes problematicus* from Rock Bench Quarry. Abbreviations as in Table 1. All measurements in mm.

Tooth Position	Parameter	N	OR	$\bar{X}$	S	V
Upper Dentition						
P^4	L	1		2.4		
	W	1		2.9		
M^1	L	3	2.4–2.5	2.43	0.06	2.4
	W	3	3.4–3.6	3.47	0.12	3.3
M^2	L	2	2.4–2.5	2.45		
	W	2	3.8–3.8	3.85		
M^3	L	2	1.9–2.0	1.95		
	W	2		3.5		
Lower Dentition						
C_1	L	3	1.1–1.5	1.37	0.23	16.8
	W	3	0.8–0.9	0.83	0.06	7.0
P_2	L	3	0.8–1.0	0.93	0.12	12.4
	W	3	0.6–0.7	0.67	0.06	8.6
P_3	L	24	1.3–1.9	1.67	0.16	9.6
	W	24	0.8–1.1	0.97	0.09	9.5
P_4	L	45	2.1–2.5	2.28	0.11	4.8
	W	45	1.1–1.7	1.40	0.15	10.8
M_1	L	61	2.2–2.7	2.47	0.09	3.8
	W	61	1.3–2.0	1.71	0.13	7.8
M_2	L	57	2.4–2.9	2.58	0.12	4.7
	W	57	1.5–2.2	1.87	0.13	7.1
M_3	L	40	2.7–3.2	2.98	0.11	3.8
	W	40	1.4–1.8	1.65	0.11	6.7

Table 4. Summary Statistics for *Plesiolestes* from Swain Quarry (from Rigby, 1980). Abbreviations as in Table 1. All measurements in mm.

Tooth Position	Parameter	N	OR	$\bar{X}$	S	V
Upper Dentition						
P^4	L	37	2.15–2.65	2.34	0.13	5.5
	W	37	2.20–3.00	2.54	0.18	6.9
M^1	L	15	2.35–2.80	2.46	0.12	4.7
	W	15	3.15–3.40	3.29	0.09	2.6
M^2	L	30	2.25–3.90	3.68	0.18	5.0
	W	30	3.40–3.90	3.68	0.18	5.0
M^3	L	22	1.40–1.65	1.58	0.07	4.1
	W	22	2.95–3.25	3.13	0.08	2.6
Lower Dentition						
P_4	L	32	2.10–2.40	2.20	0.09	4.0
	W	32	1.20–1.45	1.35	0.07	5.0
M_1	L	52	1.65–2.55	2.37	0.08	3.5
	W	52	1.65–1.90	1.73	0.09	5.1
M_2	L	53	2.25–2.55	2.39	0.09	3.8
	W	53	1.65–2.05	1.83	0.11	6.2
M_3	L	28	2.40–2.80	2.60	0.11	4.1
	W	28	1.40–1.65	1.54	0.08	4.9

Table 5. Summary statistics for *Plesiolestes* from Tongue River Localities. Abbreviations as in Table 1. All measurements in mm.

Tooth Position	Parameter	N	OR	$\bar{X}$	S	V
Upper Dentition						
M^1	L	4	1.9–2.4	2.15	0.24	11.1
	W	4	2.6–3.3	3.00	0.32	10.5
M^2	L	2	2.1–2.5	2.30		
	W	2	3.4–3.5	3.45		
M^3	L	2	1.9–2.0	1.95		
	W	2	3.0–3.2	3.10		
Lower Dentition						
P_3	L	2	1.6–1.8	1.70		
	W	2	0.8–1.0	0.90		
P_4	L	8	1.9–2.3	2.10	0.15	7.2
	W	8	1.2–1.3	1.23	0.05	3.8
M_1	L	13	2.2–2.3	2.26	0.05	2.2
	W	13	1.4–1.7	1.53	0.09	6.2
M_2	L	10	2.3–2.5	2.39	0.07	3.1
	W	10	1.4–1.9	1.68	0.13	7.8
M_3	L	9	2.5–3.1	2.80	0.18	6.4
	W	9	1.3–1.7	1.58	0.13	8.7

highly variable, as has been suggested before, and clearly differentiate *P. problematicus*. Those Rock Bench specimens which seemed to indicate a great degree of variation in P_4 morphology, for instance, a simple P_4 trigonid and weak talonid basin, do not represent *P. problematicus*, but belong to the palaechthonine genus *Premnoides*. *P. problematicus* is the only middle Paleocene palaechthonid genus with adequate sample sizes to truly reflect its variation. I believe that it is clearly distinct from, not only palaechthonines, but also from *P. nacimienti*.

Plesiolestes nacimienti (Wilson and Szalay, 1972)

Palaechthon nacimienti Wilson and Szalay, 1972, p. 5, fig. 2–10; Kay and Cartmill, 1977, p. 21, fig. 2,4,8, Pl. 1; Szalay and Delson, 1979, p. 44, fig. 14c, 15a-c; Conroy, 1981, p. 164; Taylor, 1981, p. 25; Tsentas, 1981, p. 272.

cf. *Palaechthon* sp. (in part), Tomida and Butler, 1980, p. 793, Pl. 2, fig. 2.

Paromomyid gen. and sp. indet., Tomida and Butler, 1980, p. 794, Pl. 2, fig. 1.

Talpohenach torrejonius Kay and Cartmill, 1977, p. 45, fig. 9; Taylor, 1981, p. 259; Tsentas, 1981, p. 272.

Holotype.—UKMNH 9559, left mandible with P_3-M_3 and right mandible with P_3-M_2.

Age and Distribution.—Known only from Kutz Canyon, Angel's Peak faunules, Torrejonian (middle Paleocene), San Juan County, New Mexico, and possibly from Dragon Canyon (early Torrejonian), Emery County, Utah.

Emended Diagnosis.—Differs from *P. problematicus* by having less well developed talonids on $P_{3\text{-}4}$, by having less well developed mesoconids on lower molars, by having less well developed M_3 talonids, by having less well developed paraconids on lower molars, and by having more distinct hypocones and precingula on upper molars.

Table 6. Summary statistics of Shotgun Local Fauna Plesiadapiformes. Abbreviations as in Table 1. All measurements in mm. Statistics by taxon.

Tooth Position	Parameter	N	OR	$\bar{X}$	S	V
Plesiolestes cf. *P. problematicus*						
P_4	L	6	2.1–2.3	2.23	0.08	3.7
	W	6	1.1–1.4	1.27	0.10	8.1
M_1	L	11	2.1–2.4	2.25	0.11	5.0
	W	11	1.4–1.8	1.63	0.12	7.3
M_2	L	1		2.40		
	W	1		1.8		
M_3	L	1		2.50		
	W	1		1.40		
Paromomys						
M_1	L	2	2.0–2.1	2.05		
	W	2		1.40		
M_2	L	4	1.7–2.2	1.85	0.24	12.9
	W	4	1.3–1.5	1.40	0.08	5.8
M^2	L	3	1.9–2.0	1.93	0.06	3.0
	W	3	2.4–2.5	2.43	0.06	2.4
M^3	L	2		1.2		
	W	2		2.10		
Elpidophorus						
P_4	L	2	2.7–2.9	2.80		
	W	2	1.6–1.9	1.75		
Palaechthon						
M_1	L	1		2.3		
	W	1		1.5		
Palenochtha						
M_1	L	2		1.4		
	W	2		0.90		
M_2	L	1		1.40		
	W	1		1.00		
Torrejonia sirokyi						
P_3	L	2		2.7		
	W	2	1.5–1.7	1.6		
P_4	L	1		3.4		
	W	1		2.1		
M_1	L	2	3.6–3.7	3.65		
	W	2	2.6–2.7	2.65		
M_2	L	2	3.8–3.9	3.85		
	W	2		3.0		

Discussion.—Wilson and Szalay (1972) described *P. nacimienti* as a species of *Palaechthon*. They differentiated it from *Palaechthon alticuspis* based on the following characteristics: 1) P_2 smaller than lower canine; 2) P_3 with an incipient talonid; 3) P_4 talonid lingually open; 4) P_4 with smaller paraconid and no metaconid; 5) molar paraconids less medial; 6) larger than *P. alticuspis*. Kay and Cartmill (1977) noted the resemblance in relative canine size between *P. nacimienti* and *Plesiolestes problematicus*, but chose to retain *P. nacimienti* in *Palaechthon*. They further noted that *P. nacimienti* has a small, single rooted P_2, while *P. alticuspis* has a relatively larger P_2 with either two roots or fused roots. Kay and Cartmill also noted that the type specimen of *P. nacimienti* is heavily worn and the presence or absence of a P_4 metaconid cannot be ascertained. They also noted the relatively reduced M_3, typical of this species. More recently Conroy (1981) has reviewed the Torrejonian primates from the San Juan Basin and retained *P. nacimienti* in *Palaechthon*.

Upon further examination of the characteristics mentioned above, *P. nacimienti* is not very different from *Plesiolestes*, as tacitly suggested by Kay and Cartmill (1977). As cited above and elsewhere (Kay and Cartmill, 1977; Conroy, 1981; Clemens, 1974, and others) a relatively large canine is probably primitive for plesiadapiforms. The retention of a large canine in *P. problematicus* and *P. nacimienti* is therefore not indicative of special relationships. However, the retention of a large canine and the reduction of P_2 may, and I believe does, constitute a shared and derived condition in these two taxa. *Palaechthon* shows an opposite trend in development of these teeth, with retention of a relatively large P_2 and an advanced, reduced canine (see Figure 7).

As noted by Kay and Cartmill (1977), P_2 in *Palaechthon* is nearly as large as P_3 and is usually taller, although it is also usually single rooted (contra both Simpson, 1937a and Kay and Cartmill, 1977). P_2 in *P. nacimienti* (as judged from the alveolus) was much smaller than P_3, a condition shared with *P. problematicus*. An incipient talonid on P_3 is also shared with *P. problematicus*.

The morphology of P_4 in *P. nacimienti*, known only from the heavily worn type, is still difficult to interpret. Wilson and Szalay (1972) describe it as lacking a metaconid and having a lingually open talonid, both characteristics of *Palaechthon*. As Kay and Cartmill (1977) state, it is difficult to determine the status of the metaconid of P_4 because of the wear. However, there is a distinct depression in the middle of the postvallid of the P_4 trigonid. This is characteristic of teeth that have a metaconid, and is normally lacking in those teeth that lack a metaconid. As for a lingually open P_4 talonid basin, this is again difficult to determine because of heavy wear, but this characteristic appears in heavily worn specimens of *P. problematicus* from both Rock Bench and the Shotgun fauna, so is not atypical of *Plesiolestes*.

Less medial molar paraconids are apparent only on the type specimen of *P. nacimienti* and then only on M_1, a condition typical of many plesiadapiforms and primates. Paraconids may appear more medial because of their lower position on the prevallid of the trigonid and also because they are more rounded and bulbous than is commonly the case in palaechthonines. The larger size of *P. nacimienti* seems to reflect an overall trend towards larger body size in plesiolestines compared to palaechthonines, although *P. nacimienti* is the smallest of the plesiolestine species.

Plesiolestes nacimienti also shows similarites to *P. problematicus* in its upper dentition. The P^4 in both species has a distinct and separate metacone and a relatively distinct parastyle. This differs from *Palaechthon* which has a relatively small metacone developed along the posterior flank of the paracone and a rather distinct and separate parastyle. Both species of *Plesiolestes* have distinct pre-and postprotocristae, while *Palaechthon* and *Palenochtha* lack a distinct postprotocristae. The preparaconule crista is not normally continuous with the precingulum in *Plesiolestes* species, while it is normally continuous in *Palaechthon* (although not often in *Palenochtha*).

Combined with morphological considerations are those of paleobiogeography and temporality. Paleobiogeographically, plesiolestines are a more southern radiation. The only known occurrences of *Torrejonia* are in New Mexico and south-central Wyoming (see below). *Plesiolestes* has a wider range, from New Mexico to southern Montana. Palaechthonines, for the most part, are restricted to more northern areas, specifically Montana, although *P. woodi*, if it is a palaechthonine, is represented almost solely from southern Wyoming and New Mexico (except for one tooth referred to this species by Gingerich, Houde, and Krause, 1983, from the Bangtail locality in Montana).

There is some evidence to suggest that the Kutz Canyon fauna may be slightly earlier in time than either the Torreon Wash or Gidley and Rock Bench Quarry samples. The Kutz Canyon faunule is representative of the "Deltatherium zone" fauna (To2, Archibald, et.al., 1987) as defined by Sinclair and Granger (1914), and later revised by Wilson (1951 and 1956). The Torreon Wash, Gidley Quarry, and Rock Bench Quarry samples are representative of "Pantolambda zone" faunas (To3, Archibald, et.al., 1987). Wilson (1951), Matthew (1937), and Russell (1967) all concluded that there is little temporal separation between these two zones, but were only restricted by facies differences.

Taylor (1977, 1981), Taylor and Butler (1980), and Lindsay, Butler, and Johnson (1981) have suggested that there may be some temporal element to the division of these faunas. In the San Juan Basin, the Kutz Canyon faunule, based on paleomagnetic stratigraphy is bracketed by magnetic anomalies 27 and 26 (although a few of the localities are in normal polarity anomaly 27), while it is believed that the Torreon Wash samples are in normal magnetic anomaly 26. Taylor (1977) and Taylor and Butler (1980) point out that there are no apparent lithological differences between these two areas that should occur if there were appreciable facies differences.

Butler, Lindsay, and Gingerich (1980), and Butler, Gingerich, and Lindsay (1981) present paleomagnetic data for the Clark's Fork Basin sediments. Rock Bench Quarry can only be said to be from below anomaly 26. The lower

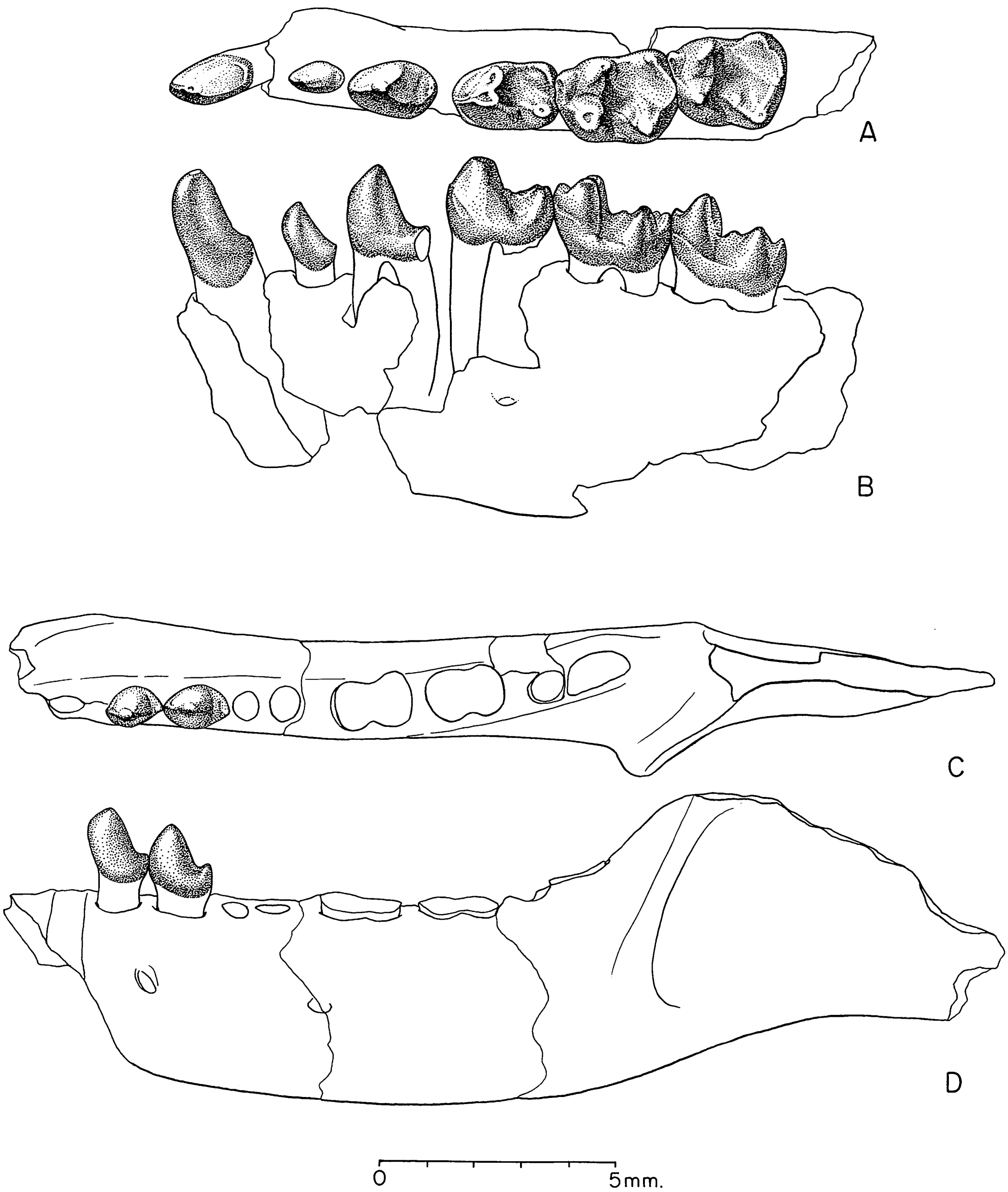

Figure 7. Relative canine and P_2 size in *Plesiolestes* and *Palaechthon*. A, YPM-PU 14836, left mandible of *Plesiolestes* with C_1, P_2-M_2. Note primitive large canine and reduced P_2. B, same in lateral view. C, AMNH 35482, right mandible (reversed for comparison) of *Palaechthon* with P_{2-3}, alveoli for C_1, P_4-M_3. Note unreduced P_2 and small canine alveolus. D, same in lateral view.

portion of the Paleocene (Puercan and Torrejonian Land-Mammal Ages) are compressed into about 150 meters of section in the Clark's Fork Basin, while the late Paleocene (Tiffanian Land Mammal Age) is represented by over 700 meters of section, indicating the probability of either greatly reduced sedimentation rates during the the first two-thirds of the Paleocene or the presence of unconformities between these Land-Mammal Ages. Also the lithology of this 150 meters of section is dominated by eroded massive sandstones, which makes accurate paleomagnetic sampling difficult (see Butler, Lindsay, and Gingerich, 1980) and renders a more precise positioning of Rock Bench Quarry impossible.

Based on the available biostratigraphic and paleomagnetic data, it is tempting to suggest that the Kutz Canyon faunule that includes *Plesiolestes nacimienti*, is slightly older than either Rock Bench Quarry or Gidley Quarry. However, the evidence still does not indicate whether the differences observed between the "*Deltatherium* zone" and the "*Pantolambda* zone" faunas reflect facies differences, time-transgressive facies differences, or temporal differences (for recent, more complete reviews of this problem see Tsentas, 1981, Archibald, et.al., 1987).

If there are temporal differences between these two faunas, *Plesiolestes nacimienti* can be viewed as the earliest plesiolestine, and the most primitive based on morphology. Tomida and Butler (1980) describe two teeth (UALP 11041 and UALP 11042) of a palaechthonid from Dragon Canyon in Utah. I have assigned both of these teeth to *Plesiolestes nacimienti*. The only difference between the two Dragon Canyon teeth and those of *P. nacimienti* is the presence of a double lobed lingual border on one of the Utah specimens. They resemble *P. nacimienti* in all other morphological details. The presence of these specimens in the Dragon fauna supports the contention that *P. nacimienti* be recognized as the earliest known plesiolestine.

Torrejonia Gazin, 1968

Torrejonia Gazin, 1968, p. 632; 1969, p. 6; 1971, p. 28; Conroy, 1981, p. 171; Taylor, 1981, p. 259; Tsentas, 1981, p. 272.

Plesiolestes (in part), Szalay, 1973, p. 86; Szalay and Delson, 1979, p. 47.

Type Species.—*Torrejonia wilsoni.*

Included Species.—*T. wilsoni* and *T. sirokyi.*

Age and Distribution.—Torrejonian, middle Paleocene of New Mexico, and early Tiffanian, early late Paleocene, Wyoming.

Emended Diagnosis.—Differs from *Plesiolestes* by lacking either a paraconid or a metaconid on P_4, by having a P_4 talonid with hypoconid and entoconid of equal height and less open lingually than *Plesiolestes*, and by having more bulbous cusps and lower crowned teeth, particularly molars.

Discussion.—Szalay (1973) and Szalay and Delson (1979) synonymize *Torrejonia* with *Plesiolestes*, noting the variability in P_4 morphology in *Plesiolestes*. As has been demonstrated above, P_4 morphological variability in *Plesiolestes* is less than previously thought. *Plesiolestes* variability is further reduced by the removal of *P. sirokyi* from *Plesiolestes* and moving it to *Torrejonia* where it fits more comfortably based on its morphology. Putting all of these species in *Plesiolestes* as Szalay and Delson (1979) suggest (or all of them in *Palaechthon* as Rigby, 1980 suggests) ignores morphological features which suggest meaningful relationships among these taxa.

Torrejonia wilsoni Gazin, 1968

Torrejonia wilsoni Gazin, 1968, p. 632, fig. 1–2; Conroy, 1981, p. 171, fig. 7.5; Taylor, 1981, p. 259; Tsentas, 1981, p. 272.

Plesiolestes wilsoni, Szalay, 1973, p. 86; Szalay and Delson, 1979, p. 47.

Holotype.—USNM 25255, left mandible with P_3-M_2.

Age and Distribution.—Torrejonian, middle Paleocene, Nacimiento Formation, east branch of Arroyo Torrejon, San Juan Basin, New Mexico.

Diagnosis.—Differs from *T. sirokyi* in being significantly smaller.

Discussion.—Little new material has been found since the original description of *T. wilsoni* by Gazin (1968) and nothing of consequence can be added to that description (see Conroy, 1981 for a discussion and description of the only new material of definitive *Torrejonia wilsoni*).

Torrejonia sirokyi (Szalay, 1973)

Plesiolestes sirokyi Szalay, 1973, p. 79, fig. 3–5; Szalay and Delson, 1979, p. 47.

Cf. *Torrejonia wilsoni*, Gazin, 1969, p. 6, Pl. 2, fig. 7–8; Gazin, 1971, p. 28.

Holotype.—AMNH 92135, right mandible with $M_{2\text{-}3}$.

Type Locality.—Saddle locality, Fort Union Formation, Freemont County, Wyoming.

Age and Distribution.—Early Tiffanian, early late Paleocene, Wyoming. Additional localities include Keefer Hill, in the Wind River Basin, and Little Muddy Creek, in the Evanston Formation of southwestern Wyoming.

Diagnosis.—Differs from *T. wilsoni* by being larger.

Discussion.—Szalay (1973) placed *T. sirokyi* in *Plesiolestes* based on its overall similarity to that genus. As Conroy (1981) and Gingerich, Houde, and Krause (1983) point out, this is not a satisfactory assignment, based on P_4 morphology. Bown and Gingerich (1973) and Bown and Rose (1976) indicate that molariform P_4's are variable in *Plesiolestes* and ally this genus with Eocene Microsyopidae because P_4 is mutable in this family as well. Recently I (Gunnell, 1985) have shown that P_4 variability is much lower in microsyopine genera than was previously thought. The same can now be demonstrated for *Plesiolestes*. This fact negates the assignment of *T. sirokyi* to *Plesiolestes* and suggests a closer relationship with *Torrejonia wilsoni*, from which it differs only in relative size.

The only other character noted by Szalay (1973, other than tooth size), used to differentiate *P. problematicus* from *T. sirokyi* was the fact that in *T. sirokyi*, the postprotocingulum does not connect to the posterior flank of the protocone as high as it does in *P. problematicus* (where it reaches the apex of the protocone). This character is shared with *T. wilsoni*, as well. Gazin (1968) notes that, "on the posterior slope of the protocone the lingual extremity of the cingulum turns towards the apex of the protocone but does not actually reach it." This is a further similarity shared between the two species of *Torrejonia* that differentiates them from *Plesiolestes*.

Before turning to the evolutionary relationships within Microsyopoidea, I will briefly discuss the Shotgun fauna from southcentral Wyoming. I have left this fauna out of the systematic discussion to this point because the taxa known from it are slightly different from those discussed above.

SHOTGUN LOCAL FAUNA

The Shotgun Local Fauna (Patterson and McGrew, 1962) contains a rather diverse assemblage of mammals. The age of this assemblage has been the subject of considerable discussion in the literature and no satisfactory conclusions have been reached, nor has the fauna ever been completely described.

The Shotgun Butte area preserves a rather thick section of Paleocene aged rocks (Keefer and Troyer, 1964) in the Fort Union Formation of the Wind River Basin, southcentral Wyoming. The lower portion of the Fort Union ranges in thickness from 500 to 1200 feet and consists mostly of sandstone and conglomerate (Keefer and Troyer, 1964). This portion is unnamed. The upper portion of the Fort Union (1100 to 2830 feet thick) is divided into two members, a marginal fluviatile one, the Shotgun Member, and an offshore lacustrine one, the Waltman Shale Member. The western Shotgun Member interfingers to the east (that is, the boundary is time transgressive eastward) with the Waltman Shale Member (McGrew, 1963).

The Shotgun Local Fauna is found in the Shotgun Member of the Fort Union Formation in a channel deposit about two miles west of where the depositing stream emptied into old Waltman Lake. It is the middle horizon of three fossiliferous horizons within the Shotgun Member. The upper fossil horizon (Shotgun Butte Fauna) is characterized by *Plesiadapis*, *P.* cf. *cookei*, and is interpreted as Clarkforkian (early Eocene) in age. The middle and lower horizons (separated by approximately 90 vertical feet) contain similar faunas, although the middle horizon is more diverse (see Keefer, 1961, Keefer and Troyer, 1964, and Patterson and McGrew, 1962).

Table 7 presents an up-to-date faunal list for the Shotgun Local Fauna. This list has been compiled from the literature in most cases (from Gazin, 1961, 1971, Gingerich, 1976, 1982b, Keefer and Troyer, 1964, McGrew and Patterson, 1962, Patterson and McGrew, 1962, Rose, 1975b and Krause, 1977). I have recently examined a large sample of the plesiadapiforms from the Shotgun Local Fauna and my

Table 7. Faunal List from Shotgun Local Fauna

Table of Fauna
Multituberculata
Ptilodus sp.
Mimetodon cf. *M. silberlingi*
Ectypodus sp.
Cf. *Anacodon gidleyi*
Cf. *Eucosmodon* sp.
Catopsalis cf. *C. fissidens*
Marsupialia
Cf. *Peradectes* sp.
Insectivora
Gelastops sp.
Cf. *Diacodon* sp.
Pantolestid, cf. *Aphronorus* sp.
Pentacodon sp.
Primates?
Nannodectes intermedius
Plesiadapis sp. (?P. praecursor)
Palenochtha cf. *P. minor*
Palaechthon woodi
Palaechthon cf. *P. alticuspis*
Plesiolestes cf. *P. problematicus*
Torrejonia sirokyi
Paromomys cf. *P. depressidens*
Ignacius fremontensis
Ignacius cf. *I. frugivorus*
Elphidotarsius shotgunensis
Carpodaptes cf. *C. hazelae*
Picrodus cf. *P. silberlingi*
Condylarthra
Peryptychus cf. *P. carinidens*
Anisonchus cf. *A. sectorius*
Promioclaenus sp.
Cf. *Litomylus* sp.
Ectocion sp.
Claenodon cf. *C. ferox*
Tricentes, near *T. subtrigonotus*
Colpoclaenus keeferi
Dermoptera?
Elpidophorus cf. *E. minor*
Pantodonta
Pantolambda cf. *P. cavirictum*

conclusions concerning their affinities are included in the table. The presence of the dermopteran *Elpidophorus minor* is reported here for the first time.

Most of the non-plesiadapiform mammalian remains have been interpreted as representing a Torrejonian age for the Shotgun Local Fauna. However, most are slightly "more advanced" than is typical for their counterparts from middle Torrejonian localities like Gidley and Rock Bench

Quarries. Of the non-plesiadapiforms only the condylarths *Ectocion*, *Claenodon* cf. *C. ferox* (also known from Cedar Point Quarry, Tiffanian, among other places), and *Colpoclaenus keeferi* (listed as coming from Cedar Point Quarry by Van Valen, 1978) may suggest a Tiffanian age for this fauna. However, few of the other taxa have been well studied.

The plesiadapiforms from the Shotgun Local Fauna also have elements indicating both late Torrejonian and early Tiffanian ages. The plesiadapids were studied by Gingerich (1976). Gazin (1971) had described *Pronothodectes intermedius* from the Shotgun fauna, as well as a *Plesiadapis* species. Gingerich moved *P. intermedius* into his genus *Nannodectes* (Gingerich, 1975) and put Gazin's *Plesiadapis* sp. in *Plesiadapis praecursor*. Both of these species are also known from Douglass Quarry in Montana and both are typical of Gingerich's *Plesiadapis praecursor* zone (earliest Tiffanian) or Tiffanian zone Ti1.

Rose (1975b) has studied the carpolestid plesiadapiforms from the Shotgun fauna, concluding that this fauna was representative of latest Torrejonian age, although he was not emphatic about this placement. There are two carpolestids represented in the Shotgun fauna, *Elphidotarsius shotgunensis* and *Carpodaptes* cf. *C. hazelae*. Rose noted that the preserved teeth of *E. shotgunensis* were more advanced than earlier *E. florencae* and do suggest a trend towards *Carpodaptes* (*Carpodaptes* appears to be the direct descendant of *Elphidotarsius*). *Elphidotarsius* is a typical middle Torrejonian plesiadapiform, so an advanced species such as *E. shotgunensis* may suggest a later Torrejonian age for this fauna. The presence of *Carpodaptes* cf. *C. hazelae* (*Carpodaptes* is typical of middle Tiffanian strata) may suggest a Tiffanian age for the Shotgun Local Fauna as well.

I have recently examined a sample of 64 teeth from the Shotgun Member representing microsyopoids and paromomyids. From this sample I am able to confirm most of Gazin's (1971) previous conclusions.

Among microsyopoids, Gazin (1971) recognized the presence of the following species: the palaechthonines *Palenochtha* cf. *P. minor*, *Palaechthon woodi*, and *Palaechthon*, cf. *P. alticuspis*; and the plesiolestines *Plesiolestes*, cf. *P. problematicus* and Cf. *Torrejonia wilsoni*. *Palaechthon woodi* (see above) remains poorly known and is of little biostratigraphic use. The *Palenochtha* sample from the Shotgun Local Fauna is almost exactly like the type sample of *Palenochtha minor* from Gidley Quarry (middle Paleocene). Gazin (1971) felt that the Shotgun *Palenochtha* sample may be slightly larger than the Gidley Quarry sample, but my measurements and comparisons fail to confirm this (see Table 6 for measurements).

The presence of *Palaechthon*, cf. *P. alticuspis* at Shotgun is rather dubious. I was only able to provisionally identify one specimen from my sample as *P. alticuspis*. The specimen is a left lower M_2 (?), which differs from the type sample of *Palaechthon alticuspis* from Gidley Quarry principally in being larger and in having more rounded and bulbous cusps. In these features it resembles *Plesiolestes* more than *Palaechthon*. However, it is smaller than the specimens assigned to *Plesiolestes* from Shotgun and although worn it lacks the distinctive hypoconulid segment of plesiolestines. It is advanced over the type *P. alticuspis* sample in its larger size and more bulbous morphology and could fit in with a late Torrejonian or early Tiffanian age designation.

Among plesiolestines there is a great deal of variation in the samples assigned to *Torrejonia* and *Plesiolestes*. The *Torrejonia* material was assigned to Cf. *T. wilsoni* by Gazin (1971), although he noted its larger size. The variability in the sample is such that the size range between *T. wilsoni* and *T. sirokyi* (*T. wilsoni* being the Torrejonian representative and *T. sirokyi* being the Tiffanian representative) is spanned. In lower first molar size the Shotgun sample is nearly identical to the *T. wilsoni* type. However, in second molar size the Shotgun sample is much larger than *T. wilsoni*, nearly identical to the M_2 size exhibited in the *T. sirokyi* type material. In $P_{3\text{-}4}$ size, the Shotgun sample is intermediate between the types of *T. wilsoni* and *T. sirokyi*. I have chosen to group the Shotgun sample with *T. sirokyi*, although a case could be made for *T. wilsoni* as well (see Figure 8). The intermediate position of this sample would confirm a late Torrejonian or early Tiffanian age for the Shotgun Local Fauna.

The *Plesiolestes* sample is also variable in size and morphology. The sample is slightly smaller in tooth dimensions (see Table 6 for measurements) than is the type *P. problematicus* sample from Rock Bench Quarry (middle Paleocene), but the size ranges are contained within the ranges of variation of the Rock Bench sample. The morphology is more variable than is the type sample, particularly in the morphology of the upper molars. In the type sample from Rock Bench all of the upper molars known possess a well developed postprotocingulum. In the Shotgun sample, many upper molars possess a postprotocingulum that originates at the apex of the protocone (as in the type sample), while others have postprotocingula that originate lower on the posterior flank of the protocone, as in *Torrejonia*. These features again suggest that the Shotgun sample is slightly more advanced than is the type sample from Rock Bench Quarry and also would support either a late Torrejonian or early Tiffanian age.

The paromomyids also support a late Torrejonian or early Tiffanian age. Gazin (1971) reported *Paromomys*, near *P. depressidens* from the Shotgun Local Fauna. Again these specimens are virtually indistinguishable from the type sample from Gidley Quarry except that they are a little smaller than is the type sample. Gazin (1971) felt that they were slightly more advanced in morphological detail from the type sample and resembled *Phenacolemur* (here *Ignacius*) more than the Gidley Quarry *P. depressidens*.

Two other paromomyids, *Phenacolemur fremontensis* and *Phenacolemur frugivorus* were reported by Gazin

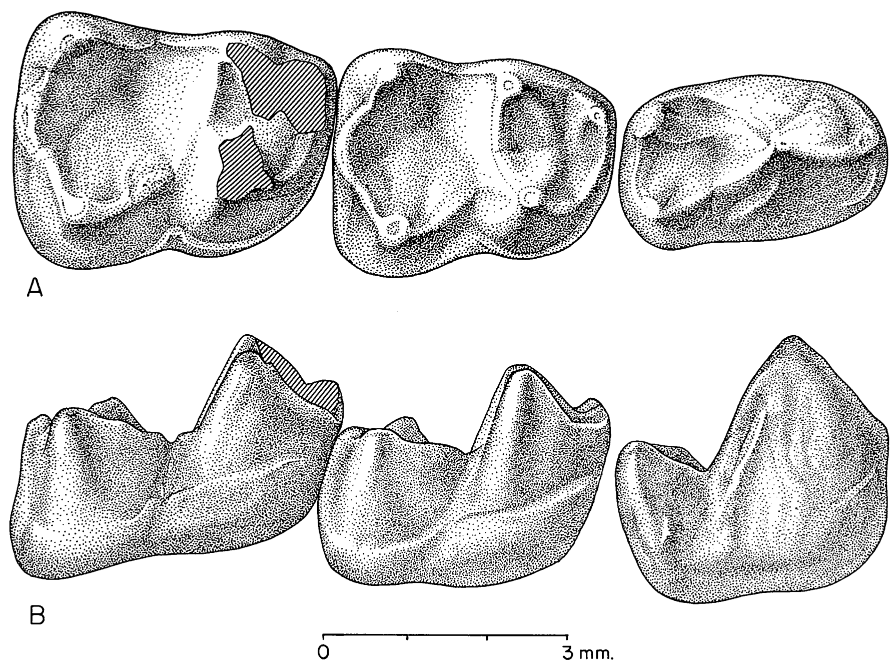

Figure 8. *Torrejonia sirokyi* from the Shotgun Local Fauna. A, MCZ 21062 and 21065 (composite), left P_4-M_2, in occlusal view. B, same in lateral view.

(1971) from the Shotgun Local Fauna. Bown and Rose (1976) correctly point out that both of these species belong in the genus *Ignacius*, not in *Phenacolemur*. Both species are similar to *Paromomys depressidens*, but differ in some details (see above). However, it is clear that *Ignacius* and *Paromomys* are very closely related. *I. fremontensis* is known only from the type specimen in the Shotgun Local Fauna, while *I. frugivorus* is present at both Scarritt and Cedar Point Quarries (middle Tiffanian) in Montana and Wyoming, respectively (see Rose, 1981a).

All of the microsyopoids and paromomyids from the Shotgun Local Fauna could be used to support either a late Torrejonian or early Tiffanian faunal age. All of the species appear more advanced than are their counterparts from other Torrejonian localities. Based solely on plesiadapiforms, an early Tiffanian age for the Shotgun sample could be supported. The earliest appearances of four genera are documented at Shotgun (*Plesiadapis*, *Carpodaptes*, *Nannodectes*, and *Ignacius*) and this first appearance datum (FAD) would be a convenient indicator of the Tiffanian Land Mammal Age (*Plesiadapis praecursor* and *Nannodectes intermedius* also appear at Douglass Quarry, interpreted as earliest Tiffanian in Montana). The other plesiadapiforms could be viewed as Torrejonian holdovers that subsequently disappeared (only *Torrejonia sirokyi* among the typical Torrejonian taxa survives into the *Plesiadapis anceps* or Tiffanian Ti2 zone).

The rest of the fauna from the Shotgun sample is not well described (or remains undescribed). It is possible that the taxa are all more advanced than are their earlier Torrejonian counterparts and could be viewed as Torrejonian holdovers into early Tiffanian time. This will remain unclear until the remainder of the fauna has been adequately described.

Another difficulty involves the preservation of the Shotgun Local Fauna. There are very few specimens that preserve mandibles or maxillae, the overwhelming majority of the sample being isolated teeth and broken bones. McGrew (1963) had suggested that the Shotgun sample represented crocodile fecal concentrations, which he felt accounted for the breakage and erosion. Fisher (1981a, b) demonstrated that the mode of preservation at Shotgun was not consistent with crocodile fecal matter, nor was it likely to have been fecal concentrations from mammalian carnivores. Fisher (1981b) preferred to interpret the concentration as a result of a death-burial-exhumation-reburial sequence accomplished under aqueous conditions. Death and initial burial would facilitate the breakdown of organic remains, after which exhumation by stream action, transport, reburial and mineralization would account for the breakage and erosion exhibited in the sample. The lack of relatively complete specimens makes taxonomic assignments more difficult.

A further complicating factor (see McGrew, 1963, Rose, 1975b) concerns the paleoenvironmental setting of the Shotgun Local Fauna. Included in the Shotgun fauna are a great number of shark teeth, at a much higher concentration than is evident at any other Paleocene mammal locality (McGrew, 1963). This suggests that sources of salt water must have been rather close during the time of the Shotgun depositional event (McGrew suggests a remnant of the Cannonball Sea) and may have meant that Waltman Lake was saline (at least in low concentrations). There is other evidence, such as the almost complete lack of *Lepisosteus*, the freshwater gar, in the Shotgun assemblage, which also supports a saline Waltman Lake. Gars are very common in almost all other freshwater Paleocene and Eocene deposits. This suggests that the paleoenvironment sampled by the Shotgun Local Fauna may have been fundamentally different from those sampled by more freshwater environments and could also reflect a different mammalian community from those of freshwater communities.

To summarize, the Shotgun Local Fauna seems to represent a transitional Torrejonian-Tiffanian fauna with taxa typical of both land mammal ages being present. A first appearance datum, based on plesiadapiforms indicates that an early Tiffanian age is likely for these strata, and I favor interpreting the Shotgun Fauna as such at least until the remainder of the fauna has been more thoroughly studied. Other factors such as little stratigraphic or locality information, the incomplete nature of the preserved material, and the evidence for an unusual paleoecological setting all compound the difficulties in assigning a definitive age to this sample.

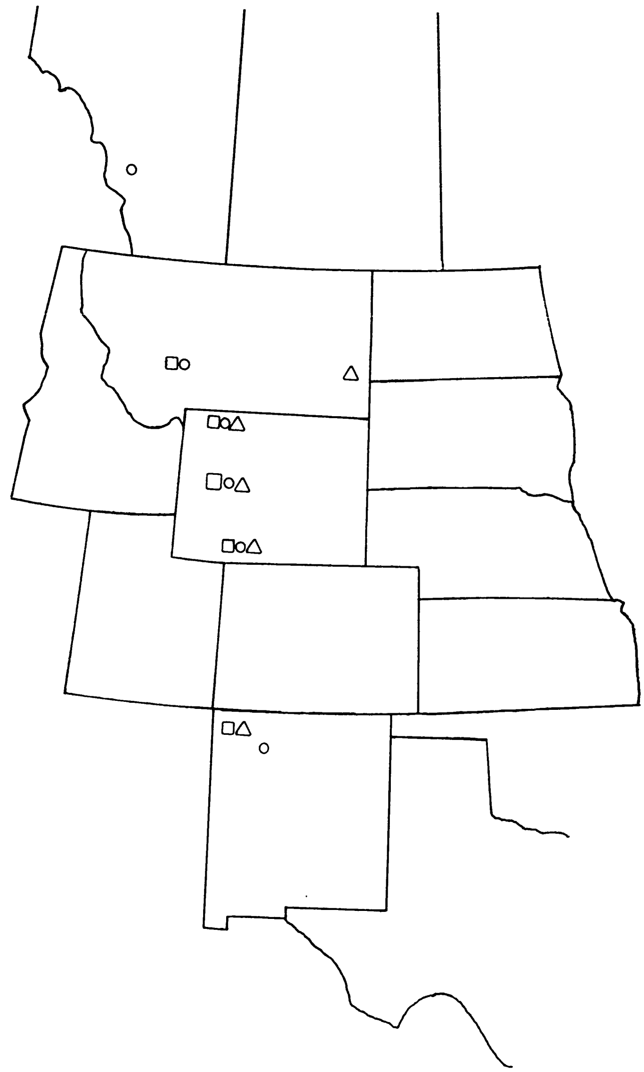

Figure 9. Geographic distribution of Torrejonian aged plesiadapiforms. Open circles represent paromomyids, open squares represent palaechthonines, and open triangles represent plesiolestines.

EVOLUTIONARY RELATIONSHIPS OF MICROSYOPOIDEA

The plesiadapiform superfamilies, Plesiadapoidea and Microsyopoidea are widespread temporally and geographically through the Paleocene of North America, with the former superfamily being fairly widespread in Europe, as well. However, there are differences in temporal and spatial distributions for the two superfamilies.

Figures 9 and 10 show the distribution of Torrejonian aged localities which contain plesiadapoids and microsyopoids. Plesiadapoids are restricted to northwestern Wyoming and southwestern Montana, for the most part. Only two of these localities have relatively good samples (Gidley Quarry for *Pronothodectes matthewi* and Rock Bench Quarry for *Pronothodectes jepi*). Of the remaining localities, only the Medicine Rocks-Tongue River record is of undoubted Torrejonian age with *Pronothodectes matthewi* (see Gingerich, 1976) and *Elphidotarsius* cf. *E. florencae* (see Rose, 1975b) being represented. Cochrane Site II in Alberta is interpreted by Krause (1978) to be late Torrejonian, based on the presence of *Pronothodectes* and *Paromomys*, however, he also notes the presence of an *Elphidotarsius* species that is more advanced than either *E. florencae* or *E. shotgunensis*, which could indicate an early Tiffanian age. Gingerich (1982b) indicated that a previously described specimen of *Meniscotherium semicingulatum* from Cochrane Site II is instead a specimen of *Ectocion collinus* and supports an early Tiffanian age for that locality. The Shotgun Butte-Keefer Hill localities are difficult to place temporally based on mammalian biostratigraphy, but are interpreted here as earliest Tiffanian (see discussion above). In summary, Torrejonian plesiadapoids are essentially only known from Gidley and Rock Bench Quarries, with a few specimens recorded from the Medicine Rocks.

Microsyopoids are more diverse, both taxonomically and geographically during the Torrejonian. While plesiadapoids are represented during the Torrejonian only by *Pronothodectes* (two species) and *Elphidotarsius* (one or

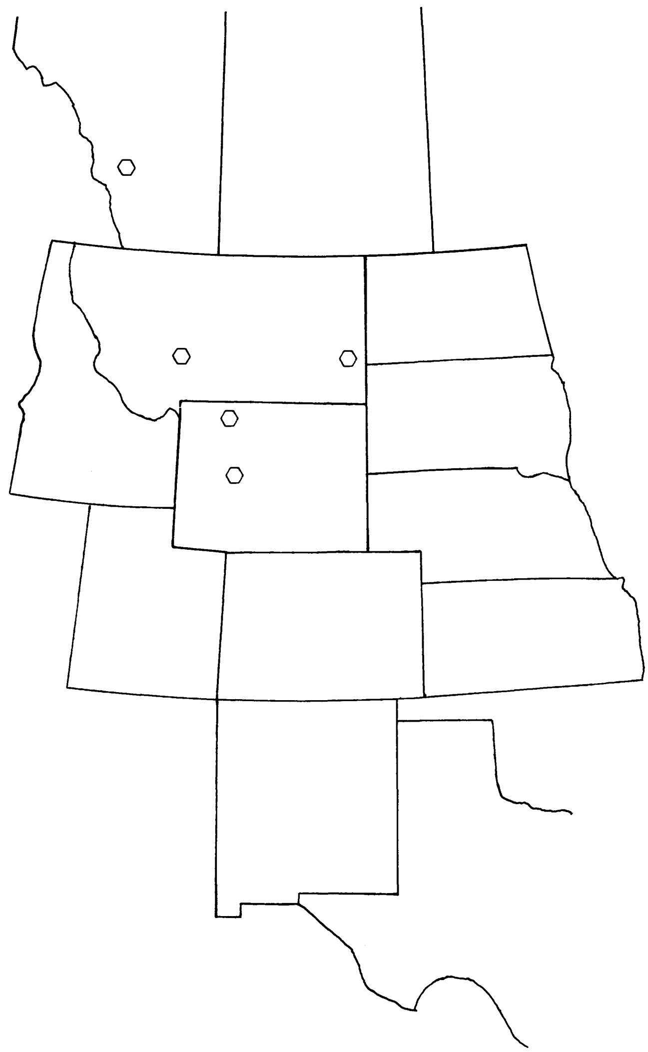

Figure 10. Geographic distribution of Torrejonian aged Plesiadapidae.

possibly 2–3 species), microsyopoids are represented by *Palaechthon* (one, possibly two species), *Palenochtha* (two, possibly three species), *Plesiolestes* (2 species), *Premnoides* (one species), and *Torrejonia* (2 species). Geographically, microsyopoids are known from definitive Torrejonian sites in New Mexico (Kimbeto Arroyo, which is probably Dragonian (*Periptychus/Tetraclaenodon* Interval Zone, To1, Archibald, et.al., 1987), Kutz Canyon, and Torreon Wash), Wyoming (Rock Bench Quarry and Swain Quarry), and Montana (Gidley Quarry and Medicine Rocks). They are also present at the probable early Tiffanian sites of Cochran Site II and Keefer Hill.

By the early Tiffanian *Plesiadapis praecursor/Plesiadapis anceps* Lineage Zone (Ti1) both superfamilies are restricted to Montana and Wyoming, from the same five regional areas; Scarritt Quarry (also Douglass Quarry for plesiadapoids) and Bangtail in Montana, and Keefer Hill, Little Muddy Creek, and Bison Basin Saddle in Wyoming. Plesiadapoids of early Tiffanian age are also known from the Medicine Rocks localities of Seven-Up Butte, White Site, and Highway Blowout (Gingerich, 1976). Taxonomic diversity has increased within Plesiadapoidea and includes the following genera; *Elphidotarsius* (one species), *Carpodaptes* (one or two species), *Plesiadapis* (two species), and *Nannodectes* (two species).

Microsyopoidea show a relatively sharp decrease in diversity after the earliest Tiffanian. Arranging the above localities temporally, the earliest Tiffanian localities (Ti1 or *Plesiadapis praecursor/Plesiadapis anceps* Lineage Zone) are Keefer Hill-Shotgun Butte, Douglass Quarry, Little Muddy Creek, and Bangtail, while the late early Tiffanian (Ti2 or *Plesiadapis anceps/Plesiadapis rex* Lineage Zone) localities are Scarritt Quarry, and Saddle Locality (the Medicine Rocks localities of Highway Blowout, Seven-Up Butte, and White Site were interpreted as Ti2, but have recently (Strait and Krause, 1988) been moved to Ti3). Of the *P. praecursor/Plesiadapis anceps* Lineage Zone localities, only Keefer Hill-Shotgun Butte preserves a rich microsyopoid fauna (4–5 genera and 6–7 species), while at the other three localities microsyopoids are reduced to two species at Bangtail (*Plesiolestes problematicus* and *"Palaechthon" woodi*, see Gingerich, Houde, and Krause, 1983), to one (*Torrejonia sirokyi* at Little Muddy Creek), and are not represented at all in the Douglass Quarry fauna (Krause and Gingerich, 1983).

In the Ti2 or *Plesiadapis anceps/Plesiadapis rex* Lineage Zone localities of Scarritt Quarry and Saddle locality, the diversity of microsyopoids remains low. At the Saddle locality microsyopoids are represented only by *Torrejonia sirokyi* (Gazin, 1956, 1969; Szalay, 1973), while at Scarritt Quarry no microsyopoids are present.

Figure 11 shows the distribution of plesiadapoids and microsyopoids through the later Tiffanian (zones Ti3 to Ti6, or *Plesiadapis rex/Plesiadapis churchilli* Lineage Zone through *Plesiadapis gingerichi*/Rodentia Interval Zones, see Gingerich, 1976, 1983a, Archibald, et.al., 1987). Plesiadapoids have a wide geographic diversity, while microsyopoids are essentially gone from this time interval. Most of the localities are clustered in Wyoming and Montana.

Figure 12 shows species richness broken down by family. Paromomyids maintain a fairly constant low species richness in the Paleocene and Eocene, with only one or two species present throughout, except at Keefer Hill where two *Ignacius* species and a *Paromomys* species may exist together. Carpolestids (not shown in figure 12) also maintain a relatively steady, low species richness in the Paleocene, with a high of two species co-existing in Tiffanian zone Ti4 (*Plesiadapis churchilli/Plesiadapis simonsi* Lineage Zone).

Palaechthonids and plesiadapids become the two most diverse Paleocene plesiadapiform familiies, palaechthonids

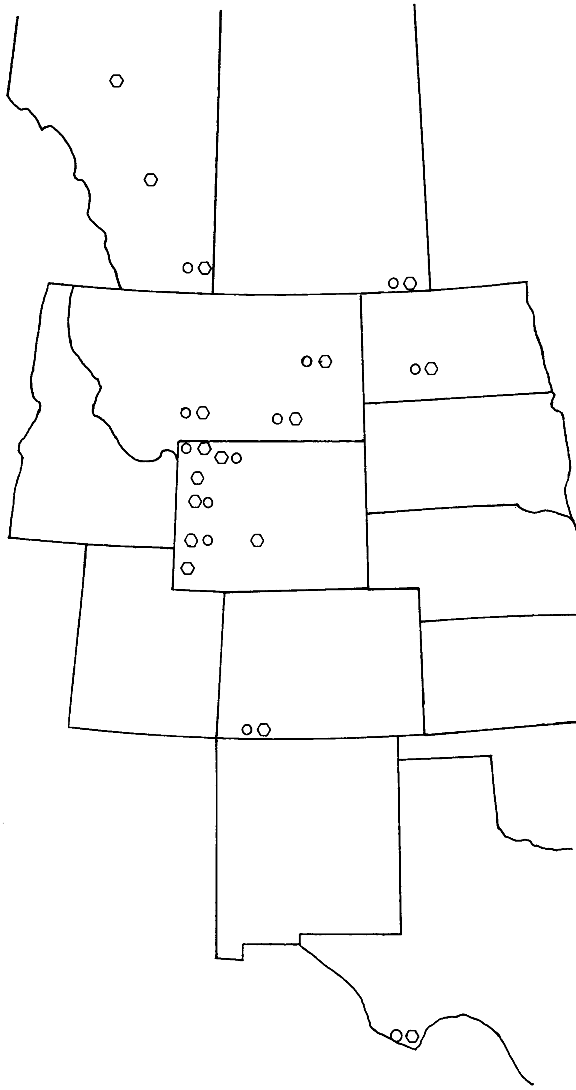

Figure 11. Geographic distribution of plesiadapiforms in middle to late Tiffanian sediments. Open circles represent phenacolemurines, open hexagons represent plesiadapids.

reaching their maximum species richness in the late Torrejonian and early Tiffanian, after which their diversity is reduced rapidly. Plesiadapids begin to increase in diversity at the time that palaechthonids are disappearing, and reach their maximum species richness in the latest Tiffanian through middle Clarkforkian, after which they too disappear rather rapidly. Plesiadapids also reach their maximum diversity in Europe at approximately the same time as they do in North America (late Thanetian, see Gingerich, 1976).

It is tempting to equate the decline of palaechthonids with the rise of plesiadapids and there may be some general correlation between these events. Palaechthonids, in general, were rather small, presumably insectivorous forms. However, their latest representatives in the early Tiffanian were larger (*Torrejonia sirokyi*) with broader, more bulbous teeth, indicating a change from complete insectivory to somewhat more of an omnivorous or frugivorous dietary preference (see Chapter VII, on body size and on tooth morphology and function). Plesiadapids underwent a general increase in body size through the Tiffanian and are characterized as being omnivorous and similar to marmots or ground squirrels (Gingerich, 1976) or to sciurids and phalangeroid marsupials (Szalay and Delson, 1979). Palaechthonids may not have been able to compete with this expanding plesiadapid radiation and may have been restricted to more southern areas at the beginning of the Tiffanian (as discussed below, climatic factors were also likely causes of reduced palaechthonid diversity). Judging from their distribution, palaechthonids were a more southerly concentrated radiation, except at the height of their diversity (late Torrejonian). They were initially represented in the Torrejonian of the San Juan Basin, New Mexico and are last known from Tiffanian Bison Basin Saddle Locality and Little Muddy Creek, both in southern Wyoming.

Sloan (1969) has recognized two terrestrial mammal communities in the North American Paleocene. The northern community existed from approximately the border of Wyoming and Colorado north into Alberta and Saskatchewan. This community is characterized by the following taxa: plesiadapoids (*Plesiadapis*, *Chiromyoides*, *Nannodectes*, and carpolestids); stylinodontine taeniodonts; hyopsodontid condylarths; and the pantodont *Titanoides*. The southern community spread southward from the Wyoming-Colorado border into New Mexico and Central America. It is characterized by the following taxa: phenacodontid condylarths; conoryctine taeniodonts; mioclaenine condylarths; mixodectid insectivores; and it appears also by palaechthonids.

For the most part, the northern radiation is represented by later Tiffanian taxa, while the southern radiation consists of taxa known mostly from the later Torrejonian through the early Tiffanian, so that these communities may represent temporal differences as well as geographic differences.

One important factor regulating these two communities may have been climate. The climate of the late Cretaceous was subtropical throughout most of the North American western interior. Near the end of the Cretaceous the climate began to deteriorate towards a more seasonable, temperate one (there is some evidence for a spike of increased temperature at the Cretaceous-Tertiary boundary), a trend that continued through most of the Paleocene (see Wolfe, 1979; Wolfe and Hopkins, 1967; and Hickey, 1980; also see Figure 13). Van Valen and Sloan (1977) note that winter temperatures became more severe and that temperate forests began spreading southward into Montana and Wyoming, replacing the earlier subtropical flora, beginning in the latest Cretaceous-earliest Paleocene. This southward expansion of temperate forests probably continued throughout

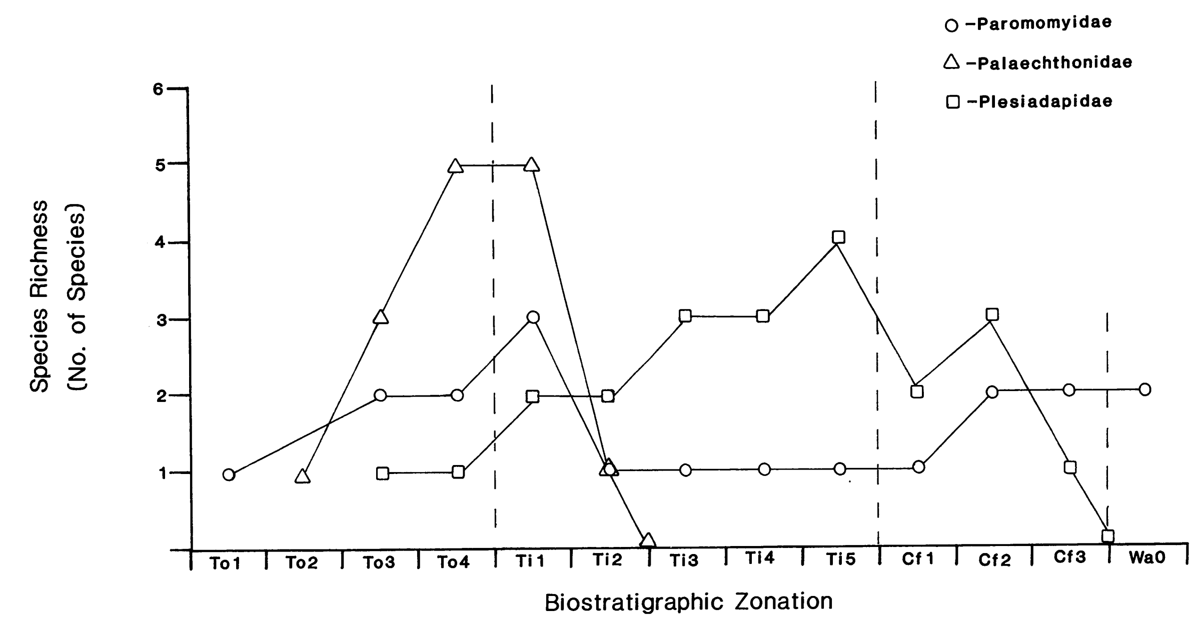

Figure 12. Species richness of various plesiadapiform families. Abscissa represents biostratigraphic zone of each family sample from early Torrejonian through early Wasatchian. Ordinate is the number of species representing each family in each zone. Open circles represent paromomyids, open triangles represent palaechthonids, and open squares represent plesiadapids. Note decrease in palaechthonid species richness co-incident with the rise in plesiadapid species richness.

most of the Paleocene, with subtropical floras returning to more northern areas (Wyoming and Montana) in the early Eocene, following increasing temperatures beginning in the latest Tiffanian and earliest Clarkforkian (Hickey, 1980).

Maas, Krause, and Strait (1988) question the timing of increasing temperatures. Based on oxygen isotope data, a case could be made for a warming trend begining in the early Tiffanian. However, this oxygen isotope information is taken from the North Sea shelf (Buchardt, 1978) and may not be representative of what was occuring in the North American western interior (Maas, et.al., 1988). Also, recent work by Kennett and Stett (1989) in Antarctica based on oxygen isotopes suggests that warming did not occur until the onset of the Eocene (middle Clarkforkian). Precise data concerning the timing of moderating temperatures in the Rocky Mountain corridor is still lacking as leaf floras provide different results as well (see Hickey, 1980; Wolfe, 1985; and Wing, 1987). New work by Wolfe (1989) supports Kennett and Stett's data from Antarctica.

Along with the southward advance of the temperate forests came a new mammalian fauna, termed the *Protungulatum* community by Van Valen and Sloan (1977). It not only replaced late Cretaceous dinosaurian communities, but also replaced the latest Cretaceous mammalian communities as well (although Archibald, 1982, does document the coexistence of these Paleocene-aspect mammals with Cretaceous mammals and dinosaurs in Garfield County, Montana).

Comparisons of the distribution through time and space of palaechthonids and plesiadapids against inferred climate

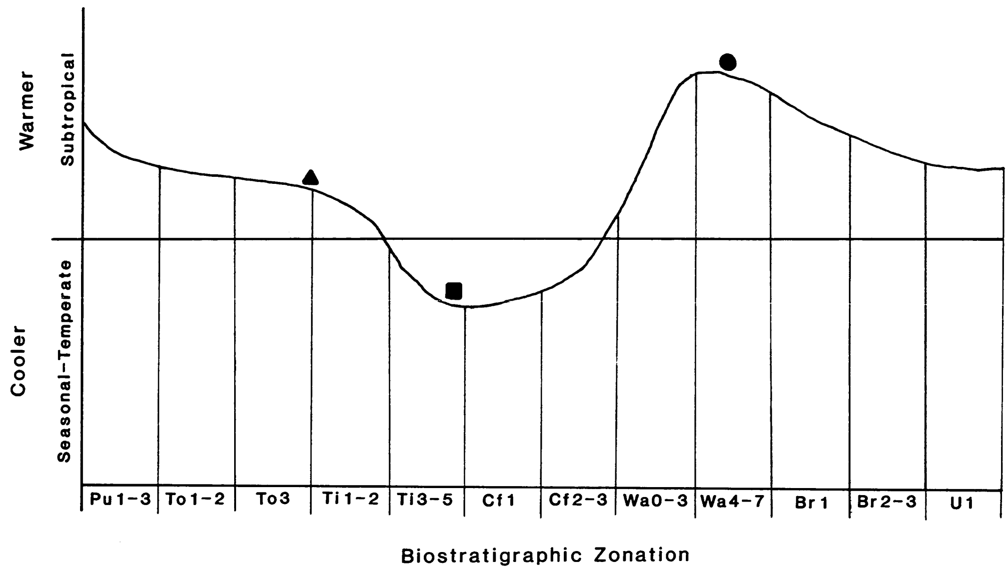

Figure 13. Paleotemperature curve for Paleocene and Eocene of North America. Abscissa represents biochronological divisions of the Paleocene and Eocene (Puercan Land Mammal Age through Uintan Land Mammal Age). For a further explanation of these biochronological divisions see Chapter 2 and Figure 3. Ordinate represents relative temperature estimates based on entire leaf margin data. Triangle represents maximum taxonomic diversity of palaechthonids. Square represents maximum taxonomic diversity of plesiadapids. Circle represents maximum taxonomic diversity of microsyopids. Figure adapted from Wolfe, 1978, Wolfe and Hopkins, 1967, Wolfe, 1989, Kennett and Stett, 1989.

are interesting. Palaechthonids are first known from the early Torrejonian of the San Juan Basin in New Mexico. Paleobotanical evidence from this area indicates that the climate was warm and humid with an abundance of subtropical plants present during this interval (Tidwell, Ash, and Parker, 1981), although Taylor (1981) believes that it might not have been as heavily forested as would be typical of tropical environments. In the later Torrejonian, palaechthonids are known from the Bighorn Basin in Wyoming and the Crazy Mountain Field in Montana. The climatological evidence for these areas is less informative. There is evidence of an overall trend towards reduced temperatures through the Paleocene in the northern fossil community, but within the Paleocene Land Mammal Ages, this trend is less clearly defined. Hickey (1980) indicates that the coolest period occurs in the Tiffanian, followed by considerable moderation of temperatures through the latest Tiffanian with a marked increase in temperature by the late Clarkforkian. Hickey (1980) feels that the cooling trend was already underway in the Puercan (agreeing with Sloan, 1969, and Van Valen and Sloan, 1977). This would suggest that Torrejonian paleotemperatures were cooler than those of the Puercan, but not as cool as those of the Tiffanian, moderated by latitudinal considerations. Thus southern Torrejonian floras should reflect warmer climatic characteristics than northern Torrejonian floras. There is little direct evidence as yet available for northern Torrejonian floras, but Hickey (1980) does note the presence of *Eucomnia serrata* and *"Cinnamomum" sezannense* from the Torrejonian of the Clark's Fork Basin, Wyoming. Tidwell, Ash, and Parker (1981) point out that *Cinnamomum* is typically present in warm, temperate rain forest type environments, suggesting that the Torrejonian temperatures of the northern community were still rather warm. However, the record of *Cinnamomum* is questionable, so it is difficult to determine with any certainty what these northern Torrejonian paleoclimates resembled, although it is possible that they were more moderate than their southern counterparts, but still rather mild compared to later Tiffanian paleoclimates.

By the early Tiffanian, palaechthonids are best known from southwestern Wyoming, near Sloan's (1969) boundary between northern and southern fossil communities (palaechthonids are also known at this time from the Bangtail locality in southern Montana). After the early Tiffanian no palaechthonids are found in either northern or southern communities.

The southward expansion of temperate forests and cooling temperatures through the Tiffanian parallel the radiation of plesiadapids. In the Torrejonian plesiadapids are restricted to northern Wyoming and Montana. By the early Tiffanian they have spread farther south into southern Wyoming and by the late Tiffanian plesiadapids are known from virtually every fauna along the Rocky Mountain corridor from Texas to Alberta. Their range begins to reduce as temperatures increase in the late Tiffanian and by the beginning of the Wasatchian Land-Mammal Age (Eocene) and the return of subtropical conditions to northern regions, plesiadapids are effectively gone.

Palaechthonids seem to have originated in, or at least are typical of, the southern terrestrial mammal community, spreading northward during the Torrejonian and then receding southward as paleoclimates continued to deteriorate through the Tiffanian. Plesiadapids seem to have originated in (or are typical of) the northern terrestrial mammal community. They were confined to the more northern latitudes during the Torrejonian (where presumably the temperatures were more moderate than in southern latitudes) and then spread southward with the southern expansion of the temperate forests of the north in the Tiffanian. Palaechthonids probably disappeared as a result of a combination of a deteriorating climate and competition (diffuse or direct) with plesiadapids, particularly with *Plesiadapis*, itself. Plesiadapids, in turn, were probably in direct competitiion with rodents (Maas, et.al., 1988) at the onset of the Clarkforkian Land-Mammal Age, and were gone from the record by the Wasatchian. The warming climate and a return to subtropical environments probably contributed to the downfall of plesiadapids.

PRIMATE AFFINITIES OF PALEOCENE PLESIADAPIFORMES

The inclusion of all of the taxa discussed above within the order Primates requires that the taxonomic and morphological boundaries of the order remain flexible and dynamic. In many ways this reflects the inability to strictly define primates even when restricting the included species to living forms only. As any primatology student soon learns, it is almost impossible to give a quick and inclusive definition of "primates" that is analogous to "odd-toed ungulates" for perissodactyls or "even-toed ungulates" for artiodactyls or "flying mammals" for Chiroptera.

In the following section I will examine the dental, cranial, and postcranial evidence available for microsyopoids, in particular, but also for plesiadapoids (as many of these characteristics are only known for plesiadapoids). This evidence suggests that plesiadapiforms are quite distinct from primates of modern aspect.

The dental evidence seems to be the least equivocal of the three. Primates tend to differ from their presumed insectivorous ancestral condition by reducing the height of the trigonid relative to the talonid, by expanding the talonid basin in length and width, as well as, depth, by reducing the puncturing aspects of their dentition (or at least concentrating this function in one or two teeth), while emphasizing the shearing and crushing aspects of their teeth. The squaring-off of upper molars reflects this trend as well, with increased trigon and talon basins and the rounding off of cusps. The earliest microsyopoids (*Purgatorius*) and plesiadapoids (*Paromomys*, *Pronothodectes*, and *Elphidotarsius*) have begun this transition from puncturing to shearing (to a lesser extent crushing) that is later even more emphasized in primates. Taxa such as *Torrejonia*, *Phenacolemur*, and *Plesiadapis* all develop crushing dentitions with puncturing and shearing often being concentrated in the incisors and usually in one or two specialized premolars (upper and lower P4 or P3–4, usually). The dental evidence for primate affinities of plesiadapiform taxa is examined in detail in Chapter VII.

CRANIAL EVIDENCE

Cranial evidence has been almost exclusively restricted to that of the basicranium. The basicranial evidence, particularly the morphology of the middle ear has long been a controversial topic among primatologists (see Van der Klaauw, 1931; Szalay, 1975, for reviews), particularly with respect to its taxonomic importance. Various aspects of this morphology have been examined including the pattern of arterial circulation through the otic fossa, the shape, position and formation of the ectotympanic annulus, the formation of the auditory bulla, and others (see McKenna, 1966; Szalay, 1975; Schwartz, Tattersall, and Eldredge, 1978). I will examine these aspects of the basicranium in the following section and attempt to determine each of these characters usefulness as a taxonomic indicator (see Figure 14 for a view of various structures).

Arterial blood supply to the middle ear capsule is accomplished by the internal carotid artery. Cartmill and MacPhee (1980) describe the presumed ancestral condition of carotid circulation in primitive eutherians as follows (see also Matthew, 1909a, and Novacek, 1977, 1980). The common carotid artery splits into internal and external branches. The external carotid artery supplies the upper neck, occiput, tongue, and lateral aspects of the face through various branchings. The internal carotid artery divides into medial and lateral branches, with the medial branch of the internal carotid entering the braincase between the petrosal and the basioccipital and emptying into the cerebral arterial circle ("Circle of Willis"). The lateral branch of the internal carotid artery travels to the posterior portion of the promontorium where it divides into a promontory artery (that travels to the cerebral circle) and a stapedial arterial branch that passes through the stapes and then divides into superior and inferior stapedial rami.

This is the commonly accepted interpretation; however, Cartmill and MacPhee (1980) and Wible (personal communication) point out that it is impossible to distinguish between the promontory branch of the lateral internal carotid and the medial internal carotid artery. There is no evidence available for mammals that indicates that both of these arteries exist in any individual and it is probable that these two arteries are homologous. The existence of a medial internal carotid artery was first proposed by Matthew in 1909 and it has remained in the literature ever since.

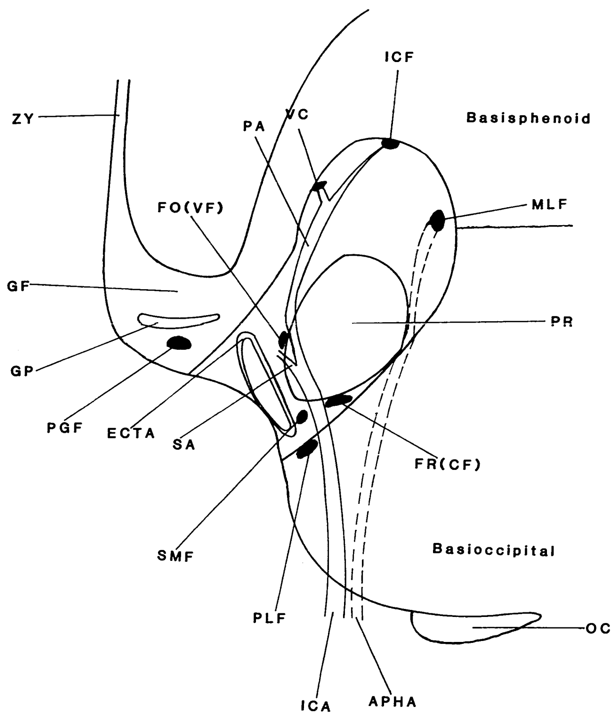

Figure 14. Schematic drawing of generalized middle ear structure, right basicranium. Abbreviations: APHA-ascending pharyngeal artery; ECTA-ectotympanic annulus; FO(VF)- fenestra ovale (or vestibular fenestra); FR(CF)-fenestra rotunda (or cochlear fenestra); GF- glenoid fossa; GP-postglenoid process; ICA- internal carotid artery; ICF-internal carotid foramen; MLF- medial lacerate foramen; OC-occipital condyle; PA- promontory artery; PGF- postglenoid foramen; PLF-posterior lacerate foramen; PR- promontorium; SA- stapedial artery; SMF-stylomastoid foramen; VC-vidian canal; ZY- zygomatic arch. Adapted from Szalay, 1975.

Gregory (1915), Szalay (1975), and Cartmill (1975) all note the presence a medial extrabullar artery (i.e., between the bulla and the basioccipital) in lorisiforms that corresponds to the expected position of a medial internal carotid. This artery has been variously interpreted as a medial entocarotid (Szalay, 1972), as an ascending pharyngeal artery (Saban, 1963, Szalay, 1975, Cartmill, 1975), or as a neomorph (that is, no homologous structure in *Homo sapiens*) by Szalay and Katz (1973). Cartmill (1975) supports the interpretation of this artery as an ascending pharyngeal (homologous to the ascending pharyngeal in *Homo sapiens*) based on the following: 1) it originates near the bifurcation of the common carotid; 2) it supplies branches to the jugular foramen, roof of the pharynx, the soft palate, and the auditory tube; and 3) it lies in close contact with the upper part of the pharynx and is crossed laterally by cranial nerves IX and XII.

Lorisiformes lack a promontory branch of the lateral internal carotid artery and their stapedial branch is reduced. This medially placed extrabullar artery can be interpreted as an ascending pharyngeal, in which case it is probably uniquely derived in lorisiforms (or may be shared with cheirogaleids as a derived state), or it can be interpreted as a medial internal carotid, which still may be homologous with the promontory branch of the lateral internal carotid since their is no evidence for the existence of a promontory artery in lorisiforms. In any event, it appears that a reduction in blood supply through the middle ear corresponds with an increased supply around the bulla and suggests that the relative sizes and positions of the middle ear arteries are less important than the resultant blood supply to the cerebral arterial circle and the facial region.

The presence or absence of a medial internal carotid artery in the primitive eutherian morphotype becomes important when primates are examined. The absence of a medial internal carotid artery is viewed as a primate synapomorphy by a number of authors (see McKenna, 1966; Szalay, 1969b, 1975; Cartmill and Kay, 1977). If the lack of a medial internal carotid artery is primitive for eutherians, then it would not be a special, derived trait linking primates. The difficulties in identifying the presence or absence of this artery (particularly in fossil forms) indicates that it is not a very taxonomically useful characteristic.

The carotid circulation in other presumed archontans (see Szalay, 1977) such as tupaiids, is similar to that of extant primates. The lateral internal carotid artery enters the bulla postero-laterally (Van Valen, 1966) and then divides into a small promontory branch and a larger stapedial branch. There is no medial internal carotid artery. This pattern is not only shared with lemuroid primates, but with erinaceomorph lipotyphlan insectivores, as well. The stapedial and promontory branches are enclosed in bony canals in both tupaiids and lemuroids. If the presumed primitive eutherian morphotype is correctly reconstructed, then only the presence of bony canals and a more postero-lateral entrance of the internal carotid into the otic region are derived. However, these may not represent special relationships between tupaiids and primates.

The fossil evidence bearing on this question is inadequate, at best; however there is some relevant material. There are some Eocene insectivore specimens that preserve the auditory region. University of Michigan specimens (UM 72623, UM 72624) of *Palaeoryctes*, a palaeoryctid insectivore (or proteutherian), have a carotid canal which enters the otic fossa posteriorly and slightly medially. *Palaeoryctes* has a rather large stapedial branch of the internal carotid and a smaller promontory branch. The stapedial branch "shields" (that is crosses ventral to and partially covers) the fenestra rotundum (cochlear fenestra), another primitive eutherian characteristic (see Archibald, 1977; Szalay, 1975). Both the stapedial and promontory branches are enclosed in bony tubes (at least, these canals are present). There is no apparent evidence of any medial internal carotid artery.

Pararyctes, a close relative of *Palaeoryctes* has a similar carotid pattern. The internal carotid enters the otic fossa posteriorly, but more medially than is seen in *Palaeoryctes*.

The stapedial artery is larger than the promontory branch as in *Palaeoryctes*, but *Pararyctes* has a promontory artery which proceeds more laterally across the promontorium than in the other genus. Neither artery in *Pararyctes* is enclosed in a bony canal and their circulatory pattern is only indicated by rather faint grooves on the surface of the promontorium.

The pentacodontid insectivoran *Aphronorus* from the early Tiffanian, late Paleocene (a specimen from the Bangtail Locality discussed above) also preserves the auditory region. In this genus, the internal carotid artery enters the otic fossa posteriorly and much more laterally than in either palaeoryctid genus. Once inside the otic fossa, there is no trace of this artery. There is no indication of either a stapedial or promontory branch. However, along the medial, dorsal surface of the promontorium there are a series of small "promontory fenestrae" which perhaps may be associated with a medially positioned internal carotid artery.

The Oligocene insectivoran *Leptictis* is perhaps the best known of fossil insectivores (see Szalay, 1969b; Gingerich, 1976). The internal carotid enters the bulla postero-medially and proceeds antero-laterally across the promontorium, dividing approximately half way across the promontorium into equally sized stapedial and promontory branches. The fenestra rotundum is not ventrally "shielded" as in palaeoryctids (it is not ventrally "shielded" in *Aphronorus* either). The stapedial, promontory, and internal carotid arteries are not enclosed in bony canals, but proceed across the promontorium in deep grooves (McKenna, 1966, notes that one specimen has a bony canal around the internal carotid before it divides into stapedial and promontory branches).

Apatemyidae, as noted by McKenna (1966), are not well known cranially, but there is evidence of a large promontory artery in a rather deep groove, somewhat similar to *Leptictis*.

Paleocene plesiadapiforms are equally under-represented in terms of evidence concerning the carotid circulation within the auditory region. Among plesiadapoids, *Plesiadapis* is relatively well-known, while *Nannodectes* is known only from one crushed skull. Among paromomyid plesiadapoids, only *Phenacolemur* and *Ignacius* are represented by cranial material that is sufficient to provide any information concerning the structures of the auditory region. No Paleocene microsyopoid is well enough known cranially to provide any information concerning carotid circulation (although some Eocene microsyopids are well enough known to provide some clues to the morphology of the Paleocene taxa, see Chapter IV).

Plesiadapis tricuspidens is represented by two rather nice skulls from Berru (the Pellouin skull and CR-125, see Gingerich, 1976) that preserve both left and right auditory regions. When Russell (1959) first described the auditory region of *P. tricuspidens* he noted that the internal carotid entered the bulla postero-laterally, just medial to the stylomastoid foramen. Inside the bulla the internal carotid "shielded" the ventral surface of the fenestra rotundum before splitting into promontory and stapedial branches of equal size, according to Russell. Szalay (1975) states that the internal carotid artery enters the bulla posteriorly then divides into a small promontory branch that is partially covered by a bony tube along its posterior aspect. The stapedial branch is very small (at least in Szalay's drawing) and there is no medial internal carotid or ascending pharyngeal artery.

Gingerich (1976) restudied all of the relevant *Plesiadapis* material and concluded that the internal carotid enters the bulla posteriorly, then "shields" the ventral aspect of the fenestra rotundum, and then continues antero-medially across the promontorium to exit the bulla through an internal carotid foramen or vidian canal. Gingerich could find no evidence of a stapedial artery and concluded that it was absent or very small and relatively unimportant. He also noted that the internal carotid artery itself was very small and that this reduced carotid circulation was probably a derived state. Gingerich also noted the lack of any bony tube or canal, refuting Szalay's earlier claim. Saban (1963) and Russell (1964) had also noted that the grooves across the promontorium were variable in size and presence, and that carotid circulation was probably reduced in *Plesiadapis tricuspidens*. Russell (1964) recanted his previous (Russell, 1959) position that the promontory and stapedial arteries were of equal size, believing instead that the stapedial was either absent or very small. Gingerich (1976) agreed with this later interpretation.

I have recently examined the Pellouin skull and can confirm Gingerich's interpretation in most regards. The internal carotid artery enters the bulla posteriorly (and slightly laterally) and then ventrally "shields" the fenestra rotundum. Gingerich states that the internal carotid then traverses antero-medially across the promontorium. It appears to me that the more probable course is antero-laterally around the latero-dorsal aspect of the promontorium, although it is not clear where it continues from there.

A new skull of *Plesiadapis cookei* (UM 87990) has been recently discovered in the Bighorn Basin of northwestern Wyoming (Gunnell and Gingerich, 1987, and in preparation). It confirms the interpretation of carotid circulation postulated for *P. tricuspidens*. A distinct groove for the internal carotid artery is located ventral to the cochlear fenestra. This groove continues antero-dorsally around the lateral surface of the promontorium. There is no indication of a stapedial artery branching off of the internal carotid. The internal carotid is not enclosed in a bony tube within the otic fossa.

MacPhee, Cartmill, and Gingerich (1983) have recently described the auditory anatomy of *Nannodectes*. It resembles *Plesiadapis* in that the internal carotid circulation seems to be greatly reduced. These authors note the presence of faint sulci on the promontoria of two *Nannodectes* specimens (one sulcus on each specimen). However, these sulci do not seem to lead to any foramina or fenestrae and are unlikely to represent or reflect the carotid circulation through the auditory fossa. The portions of the basicranium that would indicate whether or not a medial internal carotid artery or an ascending pharyngeal artery was present are not preserved in either specimen. If *Nannodectes* is similar to *Plesiadapis*, it probably lacks this arterial development. Plesiadapids may be characterized by reduced internal carotid circulation. The carotid circulation within the auditory region of paromomyids is much less well known than in plesiadapids. Only two specimens, both from the Eocene, preserve any detail. One is a specimen of *Phenacolemur* from Arroyo Blanco, New Mexico (Simpson, 1955; Szalay, 1972), while the other is a specimen of *Ignacius* (a taxon closely related to *Phenacolemur*) from the Wasatchian of the Bighorn Basin, Wyoming (MacPhee, Cartmill, and Gingerich, 1983).

Szalay (1972) described the carotid circulation of *Phenacolemur* by noting that it was difficult to determine from the specimen. However, he believed that the lateral internal carotid artery entered the bulla posteriorly and then gave off a promontory branch that continued anteriorly within a bony canal across the promontorium, this canal eventually becoming continuous with a longitudinal septum. There was no evidence for either a stapedial arterial branch or a medial internal carotid or ascending pharyngeal artery; however Szalay believed it likely that the stapedial branch existed, although small.

MacPhee, Cartmill, and Gingerich (1983) described the auditory region of *Ignacius* and compared it to Szalay's (1972) reconstruction of *Phenacolemur*. They point out that the presumed promontory bony canal described by Szalay in *Phenacolemur* is imperforate, as it is in *Ignacius* and could not therefore, have transmitted any artery. This suggests that internal carotid circulation in paromomyids was reduced as in *Plesiadapis*. However, unlike *Phenacolemur*, MacPhee, Cartmill, and Gingerich (1983) suggest that *Ignacius* may have had a rather large medial internal carotid or ascending pharyngeal artery. This is based upon the presence of bilateral apertures between the bulla and the basisphenoid, which are interpreted as medial lacerate foramina. These foramina transmit ascending pharyngeal or medial internal carotid arteries in lorisiforms, cheirogaleids, many canids, and other eutherians (MacPhee, Cartmill, and Gingerich, 1983) that contribute to the cerebral blood supply. *Phenacolemur* apparently lacks these foramina, although further fossil evidence is needed to confirm this hypothesis.

The above discussion of carotid circulation in plesiadapiforms and insectivores indicates that not nearly enough evidence exists to reach any conclusions, either taxonomically or phylogenetically. The variation and interpretive differences within both groups indicate that attempts to assign character polarities or recognize shared versus convergent character states are almost fruitless at this time. Plesiadapoidea as a whole, may share a reduced carotid circulation within the otic fossa and auditory bulla, although there are apparent differences in the presence or absence of extrabullar auditory arterial circulatory patterns. If plesiadapoids are characterized by reduced internal carotid circulation, then they share little in common with Eocene primates of modern aspect in this regard.

Carotid circulation through the auditory region of plesiadapoids differentiates them quite distinctly from Eocene adapoids and tarsioids. Reduced internal carotid circulation may represent a shared, derived character state that differentiates plesiadapoids from that of the primitive eutherian morphotype. The presence of an ascending pharyngeal artery in *Ignacius* is probably derived for that genus (and perhaps for paromomyids in general) and suggests no close relationship with other primates that share this feature (lorisids, cheirogaleids). It must be remembered, however, that not only is carotid arterial circulation likely to be highly variable, but also that it remains nearly impossible to trace definitively in fossil species.

The other aspects of the auditory region concern the form of the ectotympanic and the formation of the auditory bulla. Ectotympanic processes are one of two basic types (see MacPhee, 1981; Cartmill and MacPhee, 1980). Lemurs and tree shrews have an interbullar ectotympanic (or aphaneric in MacPhee's, 1981, terminology) that is completely enclosed within the auditory bulla. Lorises, tarsioids, and anthropoids have extrabullar ectotympanics (phaneric in MacPhee's terminology) that form part of the lateral wall of the auditory bulla and that may be extended into bony external auditory tubes as in tarsioids, *Plesiadapis*, and most anthropoids excluding South American anthropoids and the fossil anthropoids from the Oligocene of the Fayum Region, Egypt. MacPhee (1981) recognizes an additional category (semiphaneric) that is intermediate between the other two conditions. Cartmill and MacPhee (1980) believe that this semiphaneric condition is primitive for mammals. The fossil evidence bearing on this assertion is not particularly good but in the palaeoryctid insectivore *Pararyctes*, the ectotympanic exhibits this semiphaneric condition. This may support Cartmill and MacPhee's claim that semiphaneric ectotympanics were primitive for eutherians, at least.

The fossil evidence is not particularly good for any of the Paleocene primates, concerning the condition of the ectotympanic. Only *Plesiadapis* preserves an intact ectotympanic. In *Plesiadapis tricuspidens* the ectotympanic is aphaneric or interbullar (as it is in *Plesiasapis cookei*, Gunnell and Gingerich, in preparation). The ectotympanic annulus is fused to the lateral wall of the bulla by a series of bony struts, but enclosed in the bulla itself. Then the bulla continues laterally to form an external auditory tube. The ectotympanic of the paromomyid *Ignacius graybullianus* from the Eocene, also exhibited a similar condition (MacPhee, Cartmill, and Gingerich, 1983). *Phenacolemur* (Szalay, 1972) is similar to both *Plesiadapis* and *Ignacius*.

Plesiadapiform auditory regions resemble (at least superficially) tarsioid primates from the Eocene in ectotympanic construction (see Szalay, 1975, 1976), although as Gingerich (1981) has recently argued, it is probable that this similarity is convergent and not representative of special relationships between Plesiadapoidea and Omomyidae.

If semiphaneric ectotympanics and tympanic annuli which are at a low angle to the Frankfurt plane (see Archibald, 1977) are primitive for eutherians, then plesiadapoids (where known) are considerably derived from that condition. Not only is the ectotympanic intrabullar, but the ectotympanic annulus (at least in *Plesiadapis*) is at a relatively higher angle to the Frankfurt plane than is the presumed ancestral condition.

Again, as with the case of carotid circulation, caution must be taken against putting too much taxonomic importance on this character. Of all Paleocene plesiadapiforms, only three genera are represented by auditory regions complete enough to examine the ectotympanic. All of these genera are represented by derived species; for *Plesiadapis*, *P. tricuspidens*, the latest surviving Paleocene *Plesiadapis* species in Europe, and *P. cookei*, one of the latest and most derived species from North America, and for the paromomyids *Phenacolemur*, *P. jepseni* and *Ignacius*, *I. graybullianus*, both Eocene representatives of their respective genera. No evidence is available for any Paleocene microsyopoid, which dentally are more primitive than any plesiadapoid except for possibly *Pronothodectes*.

The third aspect of the auditory region that is often invoked for taxonomic purposes is the formation of the auditory bulla (the ventral covering over the otic fossa). Most authorities (see Szalay, 1975; Kay and Cartmill, 1977) agree that extant primates have a bulla formed exclusively from the petrosal, that is as an outgrowth of the petrosal element of the ear cavity. Tree shrews differ from extant primates by having an entotympanic bulla, that is, a bulla formed by a separate ossification, not as an outgrowth of one of the surrounding bony elements of the middle ear.

Cartmill and MacPhee (1980) and MacPhee (1981) document the development of auditory bullae in several mammalian species. The auditory bulla can be formed either by an outgrowth of one or several of the tympanic processes of the surrounding bones (eg. alisphenoid, basisphenoid, petrosal, etc.) or it can be formed by an entotympanic or in some cases by more than one entotympanic element, which then fuses together. By studying ontogenetic growth series MacPhee (1981) has documented the following developmental pathways. First, the tympanic cavity is enclosed by a fibrous membrane of dense connective tissue. From this stage, three different things may occur in mammals: 1) the fibrous membrane may become cartilagenous and not ossify into a bulla, but remain as cartilage throughout life; 2) a (or more than one) tympanic process of a surrounding bone (for example the petrosal) may grow out along the *inner surface* of the fibrous membrane to form the bulla. These tympanic processes are always outgrowths of their parent bones and are never formed within cartilage. Examples of this type of bulla can be seen in primates, lagomorphs, erinaceomorphs, soricomorphs, artiodactyls, cetaceans, and rodents; 3) an entotympanic may develop from a cartilagenous element that occurs *within* the fibrous membrane to form the bulla. The entotympanic normally (almost always) fuses with surrounding bones in the adult. Examples of this type of bulla can be seen in macroscelidids, carnivores, tupaiids, dermopterans, chiropterans, perissodactyls, hyracoids, pholidotans, and perhaps sirenians. Often two elements, a rostral element and a caudal element, join during ontogeny to form the complete entotympanic.

The auditory bulla of tree shrews (Cartmill and MacPhee, 1980) is composed of two to three separate elements depending upon which taxon is examined. Tupaiines have a bulla formed by a rostral entotympanic element and a caudal petrosal tympanic process. *Ptilocerus* differs from other tupaiids by having a tympanic process from the alisphenoid incorporated into the bulla along with the petrosal and entotympanic. The caudal tympanic process of the petrosal is shared between tupaiines and primates, however it is not homologous. In tupaiines, the caudal tympanic process arises cartilagenously from the mastoid region and does not surround the origin of the stapedius muscle. In lemuriforms, the caudal tympanic process of the petrosal completely encloses the origin of the stapedius muscle (a condition that may be true of all primates and may represent an autapomorphous condition for the order, although chrysochlorids may also exhibit this feature). Primates do not share the rostral entotympanic portion of the bulla with tree shrews (although they may have done so in the past, see below). Instead, the rostral portion of the primate auditory bulla is also formed by the petrosal, so that the auditory bulla is formed exclusively as an outgrowth of the petrosal in primates. A petrosal bulla has often been cited as characteristic of primates and may represent a synapomorphic character. However, as the work of MacPhee (1981) suggests, the true composition of the tympanic bulla cannot be ascertained unless growth studies are carried out for a species. Because the various elements that make up the bulla normally fuse solidly rather early in ontogeny, only juvenile or younger specimens are able to show the elements that contribute to the formation of the auditory bulla in any given case.

It is apparent that the composition of the auditory bulla cannot be ascertained without young specimens which still retain unfused auditory sutures. Only a small number of living primates of the proper developmental stages have been examined. Of these, only *Tarsius* shows any indication of an entotympanic element in its auditory bulla (Schwartz, 1978; MacPhee, 1981, questions Schwartz' interpretation). It seems that the morphocline polarity of bullar construction is still very much in doubt for living primates. Many additional taxa and more specimens of known taxa must be examined before any conclusions concerning the character polarities of the petrosal bulla in primates can be made.

As for Paleocene fossil forms, the question is clearly moot. There are very few Paleocene plesiadapiform specimens that preserve the auditory region. Of these, only the new skull of *Plesiadapis cookei* (UM 87990) is young adult. The evidence preserved in this specimen cannot refute the claim of a petrosal bulla for *Plesiadapis*. Hershkovitz (1977) claimed that *Plesiadapis tricuspidens* had an entotympanic bulla and thus should be excluded from Primates. Other authorities (most notably Russell, 1959, 1964, Gingerich, 1976, and Szalay, 1975) concluded that the bulla is formed solely from the petrosal (in the case of Russell) or, at least, is continuous with the petrosal (Gingerich, 1976). Suffice it to say that as far as *Plesiadapis* is concerned, bullar construction cannot be used to accept or reject that taxon's relationship with primates.

Other Paleocene plesiadapiform cranial remains are of little use either. The *Plesiolestes nacimienti* skull (Wilson and Szalay, 1972; Kay and Cartmill, 1977) does not preserve any of its auditory features, while the *Nannodectes* specimen (MacPhee, Cartmill, and Gingerich, 1983) does not preserve any of the bulla. The specimens of *Ignacius* (MacPhee, Cartmill, and Gingerich, 1983) and its later relative *Phenacolemur* (Szalay, 1972) show only that the bulla was continuous with the petrosal. As with *Plesiadapis*, bullar formation and composition have little or no bearing on the question of whether or not these fossil forms should be viewed as primates.

From the above discussion it is apparent that none of the aspects of the carotid region (carotid circulatory patterns, ectotympanic formation, bulla formation) are particularly useful for developing a satisfactory view of the relationship between Paleocene plesiadapiforms and primates.

POSTCRANIAL REMAINS

The postcranial skeleton of archaic Paleocene plesiadapiforms is not particularly well-known, except in the case of *Plesiadapis* (see Szalay, Tattersall, and Decker, 1975; Gingerich, 1976; Gunnell and Gingerich, in preparation). Consequently the following discussion will be limited to the known remains of *Plesiadapis*; however the implications concerning the initial radiation of primates and plesiadapiforms will be of particular importance.

The emergence of characters associated with the recognition of the order Primates (opposable hallux and pollex, nails replacing claws on digits, the development of stereoscopic vision, increased brain size and complexity, etc.) have been traditionally explained as responses to an arboreal expansion of an ancestral, primitively terrestrial insectivore group. G. E. Smith (1912) and later F. Wood Jones (1916) were first responsible for formulating this hypothesis (although Wood Jones believed that eutherians were primitively arboreal). Le Gros Clark (1959) became a powerful advocate of this idea. Stated simply, the arboreal hypothesis says that upon beginning to exploit an arboreal habitat, olfaction (while remaining a viable means of prey location) does not provide adequate means of locating suitable substrates upon which to move. Eyesight, in particular, overlapping, stereoscopic eyesight, to provide depth perception became more important and led to a reduction in the length of the snout and more closely set eyes (i.e., reduction in orbital divergence). Opposability of both the thumb and the big toe (or one or the other) became important in grasping vertical trunks and branches, which led to selection for improved hand-eye co-ordination. Tactile sensation involved in grasping are developed leading to relatively large, sensitive tactile pads on digits that are supported by broad nails instead of claws. More precise movements of hands and feet and more complex visual acuity (perhaps even color vision) required a more complex cortical development which led to the larger and more complex brains manifest in primates.

Cartmill (1974) discusses this arboreal adaptation hypothesis at length, pointing out that the obvious flaw in the arboreal hypothesis is that most arboreal mammals lack these primate specializations, thus arboreality in and of itself does not lead to these adaptations. For example, squirrels have laterally oriented orbits, lack opposability, lack relatively enlarged brains, and have claws on all digits, yet they are certainly very accomplished arborealists. Wood Jones (1916) had attempted to explain the lack of primate characters in other arboreal forms by postulating a terrestrial adaptive period within each lineage of non-primate adapted arborealists. He felt that primitive eutherians were arboreal as Matthew (1909a) had suggested. Mammals that differed from primates in arboreal adaptations had (in their evolutionary history) gone from a primitive arboreal habitat to a terrestrial habitat and then back to an arboreal habitat, acquiring arboreal characters distinct from those of primates from their terrestrially adapted ancestral forms. Evidence available today indicates that known primitive eutherians were not arboreal (see Szalay and Decker, 1974).

Cartmill (1974) argues rather convincingly that the primate characteristics cited above do not give an animal an advantage in an arboreal habitat and that other factors must be involved in the development of these characters besides arboreality. He postulates the visual predation hypothesis, in which close set eyes, grasping extremities and reduced claws, can all be viewed as responses to a visually oriented hunting adaptation. Relatively large, close set eyes allow the predator to locate its prey by sight and judge how to successfully approach the prey item. In this type of hunting, depth perception is essential to success and the development of color vision would also aid in improving the predators success ratio. Precise hand-eye co-ordination is required to quickly grasp prey items and opposability would aid in subduing and holding active prey. Finally, tactile sensation is also essential for precise manipulation of food items.

Cartmill (1974) noted that grasping hind limbs are characteristic of many small arboreal predators such as chamelions and several marsupials. Grasping hind limbs not only allow precise manipulation of prey items, they also allow careful and prolonged foraging among the slender terminal branches of trees where insects are plentiful. Forward facing, close set eyes are also seen in many hunting cats who are visual predators. The combination of cat-like eyes and chamelion-like grasping limbs characterizes the primate radiation.

Although Cartmill down plays the role of arboreality in the primate radiation, the question remains whether a primate-type of sensory system would have developed without an arboreal aspect. While vision dominated hunting is a rather wide-spread, if not common terrestrial adaptation, opposability of hallux and pollex remain nearly exclusively in the arboreal realm. Arboreality remains a prerequisite for the development of the primate visual predation hypothesis. Once the selective processes are underway, arboreality may have led to further refinements in locomotor systems of various primates (i.e., vertical clinging and leaping, or brachiation).

The postcranial remains for all Paleocene plesiadapiforms, except *Plesiadapis* (and perhaps *Nannodectes*), are based on tenuous associations between teeth and postcranial elements. Therefore only *Plesiadapis* will be discussed here in detail. Further, since arboreal adaptations are most easily recognized in the hind limbs (although upper limbs are useful as well, particularly for hanging or brachiating forms) particularly the astragalus and calcaneum, it will be these elements that will be concentrated on.

The question then becomes, can *Plesiadapis* be satisfactorily distinguished from the primitive eutherian morphotype based on the astragalus and calcaneum? Szalay and Decker (1974) Szalay and Drawhorn (1980), Decker and Szalay (1974), and Dagasto (1983) have discussed the morphological characteristics of the tarsus in primitive eutherians and archaic plesiadapiforms (as well as adapid primates) at length. They believe that differences in the locomotor substrate (trees vs. terrestrial habitats) preferences can be recognized by characteristic differences in the morphology of the ankle joint.

Certain assumptions concerning the configuration of tarsal articular surfaces must be made (Szalay and Drawhorn, 1980). The first assumption is that habitual orientation of the foot will be reflected in the joint surfaces of tarsal elements. It is assumed that joint surfaces that are in contact during the most frequently held foot positions will reflect the increased (by habitual use) forces being transmitted through them by being relatively larger in surface area than those joint surfaces that are not under habitual compressive force. A second assumption is that joint axes of rotation and movements of the tarsal elements can be inferred from the configuration of their articular surfaces.

Szalay (1977) and Szalay and Decker (1974) discuss the characteristic morphology of the primitive eutherian tarsal morphotype. Their reconstruction of the morphotype is based on tarsal elements collected from the late Cretaceous Bug Creek Anthills locality (see Sloan and Van Valen, 1965). Two genera, *Protungulatum* (an ancestral condylarth) and *Procerberus* (an ancestral palaeoryctoid insectivore) form the basis for their reconstruction of primitive eutherian tarsal morphology.

The following characters are recognized as primitive for eutherians (see Szalay and Decker, 1974): 1) a distally located peroneal tubercle of the calcaneum; 2) cuboid facet of the calcaneum obliquely oriented to the long axis of the calcaneum; 3) posterior astragalar-calcaneal facet forming a relatively large angle (35–40 degrees) with the long axis of the calcaneum; 4) a short calcaneal body anterior to the astragalar-calcaneal facet; 5) presence of a plantar anterior tubercle of the calcaneum and a groove for the anterior plantar ligament; 6) a short, low, shallowly grooved astragalar trochlea; 7) large astragalar canal; 8) sustentacular facet of the astragalus not continuous with the naviculo-astragalar facet of the astragalus; 9) a wide astragalar head thickened laterally that is dorso-laterally oriented; 10) fibula articulation with both the astragalus and calcaneum.

The above features of the tarsal joints tend to restrict movement at the ankle to predominately flexion (dorsaflexion) and extension (plantar flexion). A distally located peroneal tubercle allows for eversion of the foot (see discussion below) and indicates that the primitive eutherian foot was capable of relatively powerful eversion. The obliquely oriented cuboid facet and the relatively flat joint surfaces of the cuboid and calcaneum indicate that the axis of rotation of this joint was parallel to the joint surfaces, restricting movements at the lower ankle joint to flexion and extension. The large angle of the astragalo-calcaneal articular surfaces and the relative flatness of the joint surfaces also indicate that proximal-distal movements were predominant at this joint, and also that the joint was probably relatively stable with little movement occurring around it. A short calcaneal body anterior to the astragalar-calcaneal articulation indicates a smaller load arm to power arm ratio (power arm being the distance from the astragalar-calcaneal articulation to the proximal end of the calcaneal tubercle) and suggests that relatively powerful plantar flexion was possible in the primitive eutherian tarsal complex. A large plantar tubercle and plantar ligament groove indicate the presence of a strong plantar calcaneal-cuboid ligament, which aids in stabilizing the calcaneal-cuboid joint during dorsaflexion and strengthening the calcaneal-cuboid joint in general. A short, grooved astragalar trochlea indicates that flexion and extension were the predominant movements that occurred at this joint and that the joint axis of rotation was perpendicular to the trochlear groove. A large astragalar canal limits the range of plantar flexion at the astragalar-tibial joint (the distal tibial trochlea could not move beyond the point where the posterior surface encountered the nerves and vessels which passed through the astragalar canal without damaging them). An isolated sustentacular articular facet on both the calcaneum and astragalus suggests that these surfaces were rather closely bound together and that little movement occurred through this articulation. A laterally enlarged astragalar head indicates that relatively more compressive force is transmitted through this side of the astragalus (if we accept the assumption noted above). The navicular is typically shifted laterally when the foot is everted and compressive forces are directed through the navicular to the lateral surface of the head of the astragalus. This suggests (as does the anteriorly or distally placed peroneal tubercle) that some eversion was an important foot movement in primitive eutherians. Finally, a fibular-calcaneal articulation (along with a fibular-astragalar articulation) serves to stabilize the foot in the medial-lateral direction. Figure 15 shows the various aspects of the primitive eutherian foot discussed above and should be referred to for further explanation of the morphology and presumed movements inferred for the primitive eutherian tarsal complex.

To summarize, the primitive eutherian foot (based mostly on inferred *Protungulatum* tarsal elements) was characterized by a tibial-astragalar joint capable of strong dorsal flexion, somewhat less plantar flexion, and little or no medial-lateral movement. The calcaneal-astragalar joint was capable of some limited proximal-distal movement but was a rather stable joint in general. Both of these joints were further stabilized medio-laterally by a fibular articulation with both the astragalus and the calcaneum. The cuboid-calcaneal joint was capable of flexion and extension, while the distal peroneal process and the enlarged lateral aspect of the astragalar head indicate that some eversion was possible, although limited by the well-developed calcaneo-cuboid ligament.

Szalay and Decker (1974) suggest that this type of tarsal configuration reflects a flat, rather homogeneous locomotor substrate in which the foot is not required to change its orientation a great deal to accommodate a more diverse substrate. They interpret this type of tarsal configuration as reflecting a terrestrial adaptation, pointing out that terrestrial animals are capable of avoiding areas where more diverse foot orientations might be required.

The primitive eutherian foot seems to have been adapted for locomotion on horizontal (for the most part) substrates, although the ability to evert the foot suggests that this substrate may have been partly uneven. The habitat may have been a forest floor litter with a basic horizontal orientation, but with some more vertical substrate aspects intruding on the basic pattern. In a forest environment it is not always possible to avoid difficult substrates when searching for food, as these animals (primitive eutherians) presumably shared an insectivorous-omnivorous dietary regime. This type of avoidance may be possible in savannah or open woodland habitats where grazing or browsing is predominant, and may reflect cursorial adaptations of the tarsal complex as in horses where virtually no inversion or eversion of the foot is possible. However, primitive eutherians remain more generalized in tarsal adaptations, but were probably predominantly terrestrial.

In contrast to the condition of the tarsal complex in primitive eutherians, plesiadapiforms are quite different (at least as manifest by *Plesiadapis*). Szalay and Decker (1974) base their characterization of plesiadapiforms on a number of tarsal elements from various Paleocene localities in North America and Europe and generalize their conclusions for the entire infraorder. However, it must be pointed out that only in *Plesiadapis* is there truly associated cranial and skeletal material. *Plesiadapis* is a rather specialized genus (particularly the best known species postcranially, *Plesiadapis tricuspidens* and *Plesiadapis cookei*) and extreme caution should be taken when generalizing from *Plesiadapis* to the other members of plesiadapiforms, particularly in light of the diverse body sizes and dietary specializations exhibited by other genera within the infraorder. The following list of tarsal features, while taken as representative of plesiadapiforms in general, will without doubt, be shown to be erroneous when genera other than *Plesiadapis* are better known. *Plesiadapis* tarsal elements are characterized by the following (see Figures 16, 17): 1) peroneal tubercle large but located more proximally than in primitive eutherians; 2) cuboid facet of the calcaneum perpendicular (transverse) to the long axis of the calcaneum, rounded and concave on the calcaneum, rounded and convex on the cuboid; 3) astragalar-calcaneal facet of calcaneum forms a relatively low angle to the long axis of the calcaneum, is rounded, and is posteriorly accentuated (enlarged); 4) the anterior plantar tubercle of the calcaneum is rather large but the groove for the plantar calcaneal-cuboid ligament is reduced or lost; 5) the astragalar trochlea is higher with a high, strongly crested lateral side and a smooth rounded medial side, the trochlear groove is very shallow or flat and is extended onto the astragalar neck; 6) the astragalar canal is reduced compared to primitive eutherians; 7) the sustentacular facet of the astragalus is continuous with the astragalar-navicular facet; 8) the astragalar head is enlarged medially instead of laterally as in primitive eutherians; 9) a deep groove for the flexor digitorum fibularis tendon is present; 10) the fibula does not articulate with the calcaneum; 11) there is an enlarged rugosity for the origin of the spring ligament.

Examining these characters more closely reveals that the plesiadapiform foot was capable of a greater number of tarsal orientations compared to the primitive eutherian foot. A large peroneal tubercle (even more robust than in *Protungulatum*, but relatively smaller) suggests that eversion was still an important foot movement and orientation, although the mechanics of foot eversion differed in plesiadapiforms and primitive eutherians (see discussion below).

The transverse and rounded calcaneal-cuboid articulation combined with the convex cuboid facet and the concave calcanear facet indicate a capability for more medial-lateral rotation at this joint than was possible in the primitive eutherian foot. While the joint axis of the eutherian cal-

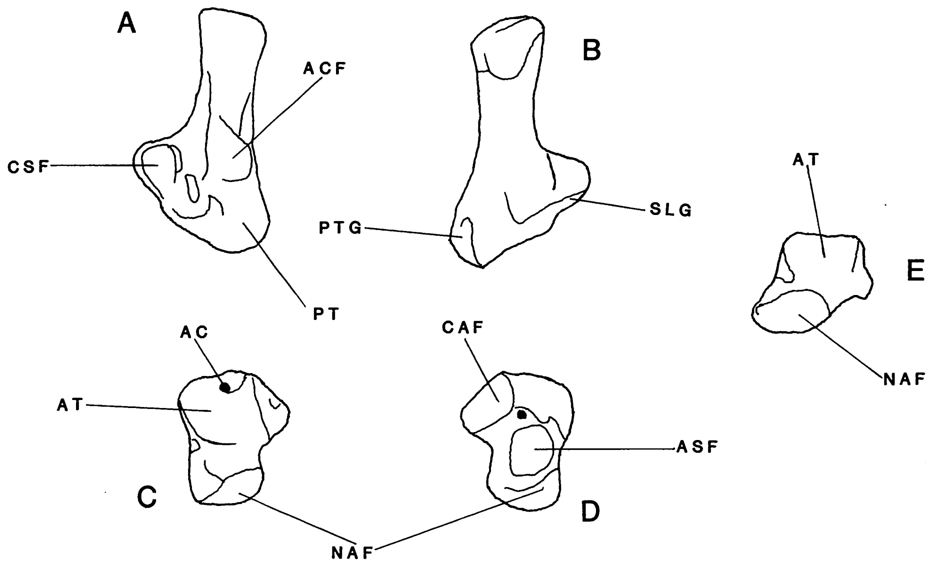

Figure 15. Characteristics of astragalar and calcanear elements of primitive eutherian foot (adapted from Szalay and Decker, 1974). A,B- calcaneum. C-E-astragalus. A,C-dorsal view. B,D- plantar view. E- distal view. Abbreviations: AC- astragalar canal; ACF- astragalar-calcaneal facet; ASF- astragalar-sustentacular facet; AT-astragalar trochlea; CAF- calcanear-astragalar facet; CSF-calcanear sustentacular facet; NAF-navicular-astragalar facet; PT- peroneal tubercle; PTG- groove for peroneus longus tendon; SLG- groove for spring ligament attachment.

caneal-cuboid articulation was parallel to the joint surface, it is nearly perpendicular to the joint surface in plesiadapiforms allowing medial-lateral rotation. Along with this, the reduction or loss of the groove for the plantar calcaneal-cuboid ligament indicates that if this ligament was present it was much reduced and would not prevent medial-lateral rotation at this joint as it did in primitive eutherians.

The angle of the calcaneal-astragalar articulation to the long axis of the calcaneum is reduced and the astragalar surface is rounded, which allows some medial-lateral movement of the middle ankle joint. The rounded surface produces a helical movement when the calcaneum is moved relative to the astragalus. The posterior aspect of the calcaneal-astragalar facet is enlarged in plesiadapiforms. When the foot is inverted the cuboid is laterally rotated shifting the navicular medially and moving the astragalus slightly posteriorly. In the inverted position the greatest compressive forces are concentrated on the medial aspect of the astragalar head and the posterior aspect of the calcaneal-astragalar articulation. Both of these areas are enlarged in plesiadapiforms suggesting that inversion was an important foot movement and that an inverted foot may have been an habitual orientation.

The shallow or flat trochlear groove of the astragalus suggests that some limited medial-lateral movement was possible at this joint, although the fibular-astragalar articulation still probably limited the majority of the movement at this joint to dorsal and plantar flexion. The extension of the groove onto the neck of the astragalus and the reduction of the astragalar canal indicate that plesiadapiforms were capable of a greater degree of plantar and dorsal flexion than were primitive eutherians. The astragalar sustentacular facet is continuous with the astragalar-navicular facet and indicates that the sustentacular articulation of the astragalus and calcaneum was not as rigid as that found in primitive eutherians and that a gliding movement was possible at this joint. This in turn allows for more medial and lateral movements at this joint.

The rugosity at the distal surface of the calcanear sustentaculum is enlarged, suggesting that the calcanear-navicular ligament, or the spring ligament was enlarged. The spring ligament aids in the stabilization of the navicular-astragalar joint, particularly during inversion and its enlargement also argues for the importance of inversion in plesiadapiforms. Finally, the deep groove for the tendon of flexor digitorum fibularis, found on the postero-medial aspect of the astragalus and the medial aspect of the calcaneum on the plantar surface of the sustentaculum suggests that powerful flexion of the digits was possible in plesiadapiforms.

To summarize, plesiadapiform tarsal elements indicate a foot capable of many more orientations than those indicated for primitive eutherians. Not only were plesiadapiforms

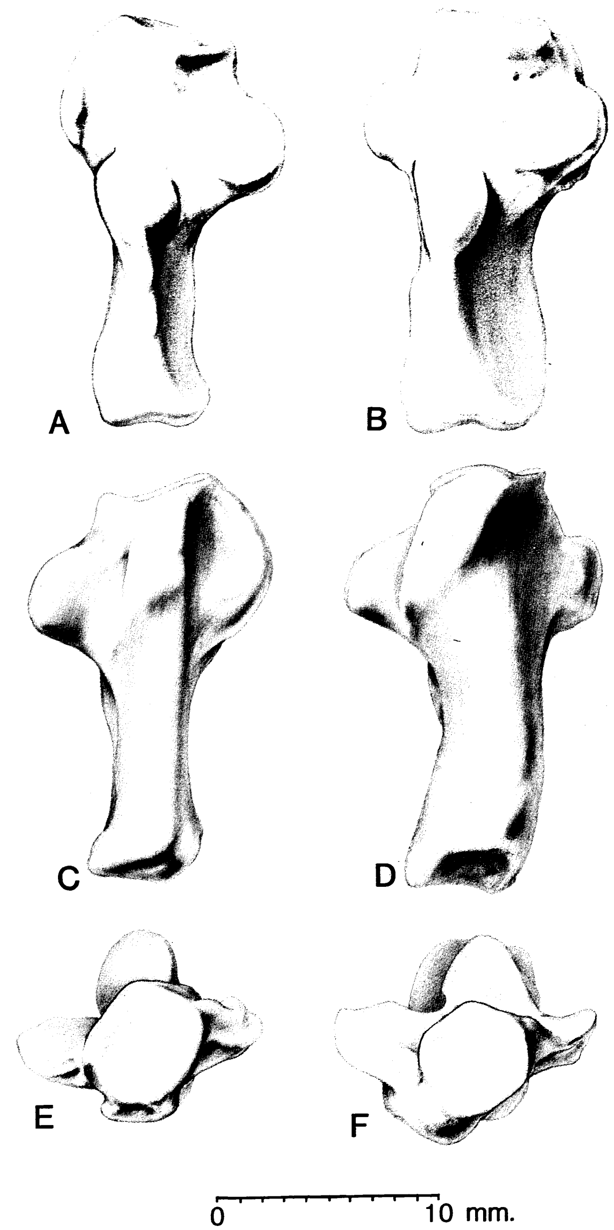

Figure 16. *Plesiadapis* and *Marmota* calcanii. A, C, E are *Plesiadapis*. B, D, F are *Marmota*. A, B in dorsal view; C, D in plantar view; E, F in distal view. See text for further explanation. Abbreviations as in Figure 15.

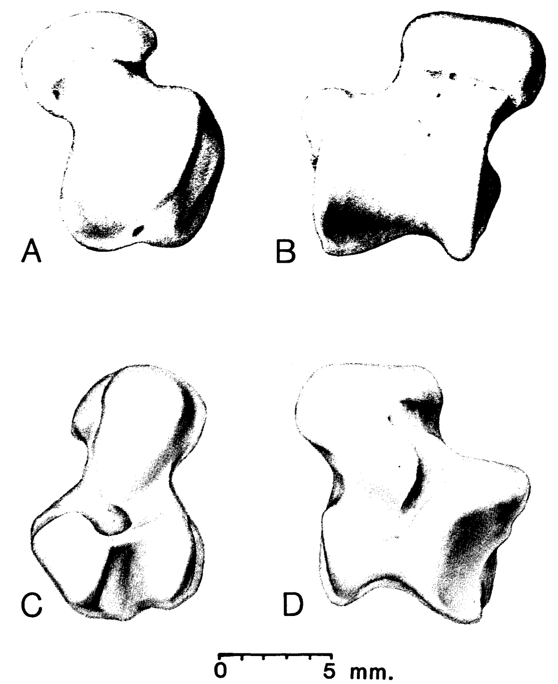

Figure 17. *Plesiadapis* and *Marmota* astragali. A, C are *Plesiadapis*. B, D are *Marmota*. A, B in dorsal view; C, D in plantar view. See text for further explanation. Abbreviations as in Figure 15.

capable of greater degrees of flexion and extension at the tibial-astragalar joint and the calcanear-cuboid joint, they also were capable of much greater eversion and inversion, particularly at the calcaneal-cuboid joint, and to a lesser degree at the calcaneal-astragalar and tibial-astragalar joints. The available evidence suggests that inversion was much more important in plesiadapiforms than in primitive eutherians and may have been the habitual orientation of the plesiadapiform foot.

Szalay and Decker (1974) equate the more mobile foot of plesiadapiforms with an arboreal adaptation. This mobility allows the arboreal animal to make use of the more heterogeneous locomotor substrates that are found upon entering into life in the trees. Szalay and Decker (1974) after Cartmill (1972) note that arboreal substrates are more discontinuous than are terrestrial ones; they are more mobile than are terrestrial substrates; they are more variable in width and are oriented at all angles to the pull of gravity. Embarking upon an arboreal life pattern would select for a more mobile foot. A habitually inverted foot could result from selection for clinging to vertical trunks and branches as could selection for more powerful flexion of digits. Szalay and Decker (1974) postulate that the plesiadapiform characteristics of the tarsus noted above are indicative of plesiadapiform arboreality. If this is true then plesiadapiforms should be considered as primates if the view that arboreality is indicative of the initial radiation of primates is accepted. As we have seen, even though Cartmill (1974) would not accept arboreality as the ultimate cause of the primate radiation, his visual predation hypothesis is only acceptable with arboreality as an integral part. If arboreality is viewed as the ultimate causal factor for the primate radiation as Szalay and Decker suggest, then plesiadapiforms should be viewed as primates. If the presence of the characteristic visual predation adaptations are viewed as indicative of primates as Cartmill suggests, then plesiadapiforms should not be viewed as primates, but as "preadapted protoprimates" (see MacPhee, Cartmill, and Gingerich, 1983, for a more recent view of Cartmill's ideas).

Another question concerns the interpretation of these plesiadapiform tarsal elements as being indicative of arboreality. As was stated above, nearly all of the material discussed by Szalay and Decker (1974), at least, all of the material definitively assigned to genus and species, is *Plesiadapis* and almost all of that is *Plesiadapis tricuspidens*, a rather large, specialized species of a rather specialized genus. Gingerich (1976) studied the limb proportions of the *Plesiadapis insignis* skeleton from Menat and concluded that *Plesiadapis* was probably ground-squirrel or marmot-like in limb proportions. Further, he noted that the limbs of *Plesiadapis* were more robust than those typical of arboreal mammals. The humerus of *Plesiadapis* also indicates that it had powerful flexor musculature. Its *teres major* tuberosity is enlarged, a condition reminiscent of moles, although moles have much more expanded tuberosities than is typical of *Plesiadapis*. All of this led Gingerich (1976) to conclude that *Plesiadapis* was primarily terrestrial and may have been a burrower, as well. He did state that it was possible that *Plesiadapis* climbed trees (marmots occasionally will climb and ground squirrels are accomplished climbers) but that its primary locomotor substrate was terrestrial in nature.

The relative size and position of the peroneal tuberosity provides clues concerning foot mobility, as well. The tendons of *peroneus longus* and *peroneus brevis* traverse the peroneal tuberosity and then insert on the base of the first metatarsal and the entocuniform, and the fifth metatarsal, respectively. Both of these muscles plantar flex and evert the foot. The peroneal tuberosity serves to orient the direction in which the forces applied by the peroneus musculature will act (see Figures 18, 19). The more distally placed the peroneal tuberosity is on the calcaneum, the more laterally oriented is the direction of the force applied by the peroneus musculature. In taxa where the direction of muscle pull is laterally oriented, the component of eversion becomes more important than the component of plantar flexion. The reverse becomes true as the tubercle moves more proximally along the lateral side of the calcaneum. Also, the relative size of the peroneal tubercle serves a similar purpose. The larger the tubercle is, the more laterally extended the peroneal tendons become before turning medially to traverse the plantar aspect of the foot.

If we examine the relative position and size of the peroneal tubercle in primitive eutherians, plesiadapiforms, and later adapids, the following pattern emerges. In *Protungulatum* the peroneal tubercle is relatively large and is developed at the distal most point of the lateral surface of the calcaneum. This position serves to orient the peroneus longus tendon relatively transversely across the plantar aspect of the foot and results in a large eversion component and a relatively smaller plantar flexion component in the action of the muscles. In the case of *Protungulatum*, this orientation may be the result of the hinge-like joint of the calcaneal-cuboid articulation that limits medial and lateral rotation at this joint. To achieve any degree of foot eversion the peroneus tendon must be directed more medial-laterally. Some degree of foot eversion seems to characterize *Protungulatum*.

In the case of *Plesiadapis* the peroneal tubercle is positioned slightly more proximally than is the case in *Protungulatum*. The tubercle itself is relatively more robust than in *Protungulatum*. The component of eversion is still relatively much larger than is the component of plantar flexion. However, it may be that the eversion component is smaller compared to *Protungulatum*. This may be the result of two related factors. First, the calcaneal-cuboid articulation has changed from a hinge-type articulation in *Protungulatum* to nested concave-convex surfaces which allow medial-lateral rotation at this joint in *Plesiadapis*. The slightly more proximal position of the tubercle may have resulted from the development of this joint system which does not require as much lateral force to evert the foot as the system in *Protungulatum*. However, the peroneal tubercle remains robust in *Plesiadapis*. If the *Plesiadapis* foot, as Szalay and Decker (1974) suggest, was habitually inverted, perhaps the relatively high component of eversion of the peroneus musculature was maintained to oppose the forces resulting from inversion and thus lead to a more stable tarsal complex. Both of these foot motions would remain important for an animal that was exploiting not only broken, uneven terrestrial habitats, but also exploiting arboreal habitats.

The peroneal tubercle of both *Adapis* and *Notharctus* (see Decker and Szalay, 1974; Dagasto, 1983) was much reduced in size and robusticity compared to *Plesiadapis* and *Protungulatum* (see Figures 18, 19). It was also positioned more proximally than in either of the above taxa (this is to some extent a result of the lengthening of the distal portion of the calcaneum, especially in *Notharctus*). In both of these taxa (*Adapis* and *Notharctus*) the tendons of the peroneal muscles would have been oriented more obliquely than is the case in *Plesiadapis* or *Protungulatum*. Consequently, the component of eversion is decreased. Both *Adapis* and *Notharctus* have developed an efficient cuboid-pivot (see Decker and Szalay, 1974) at the calcaneal-cuboid articulation and are capable of a great deal of medial-lateral rotation at this joint. A more laterally directed peroneus tendon is not required to execute eversion. Further, there is evidence to suggest that both *Adapis* and *Notharctus* had divergent, opposable halluces. By shifting the peroneal tendons proximally and more obliquely across the sole of the foot, they are in a better position to aid in opposing forces applied to the hallux. Other evidence suggests that adapids may have been arboreal quadrupeds (see Dagasto, 1983). A more obliquely oriented peroneus musculature is able to increase its contri-

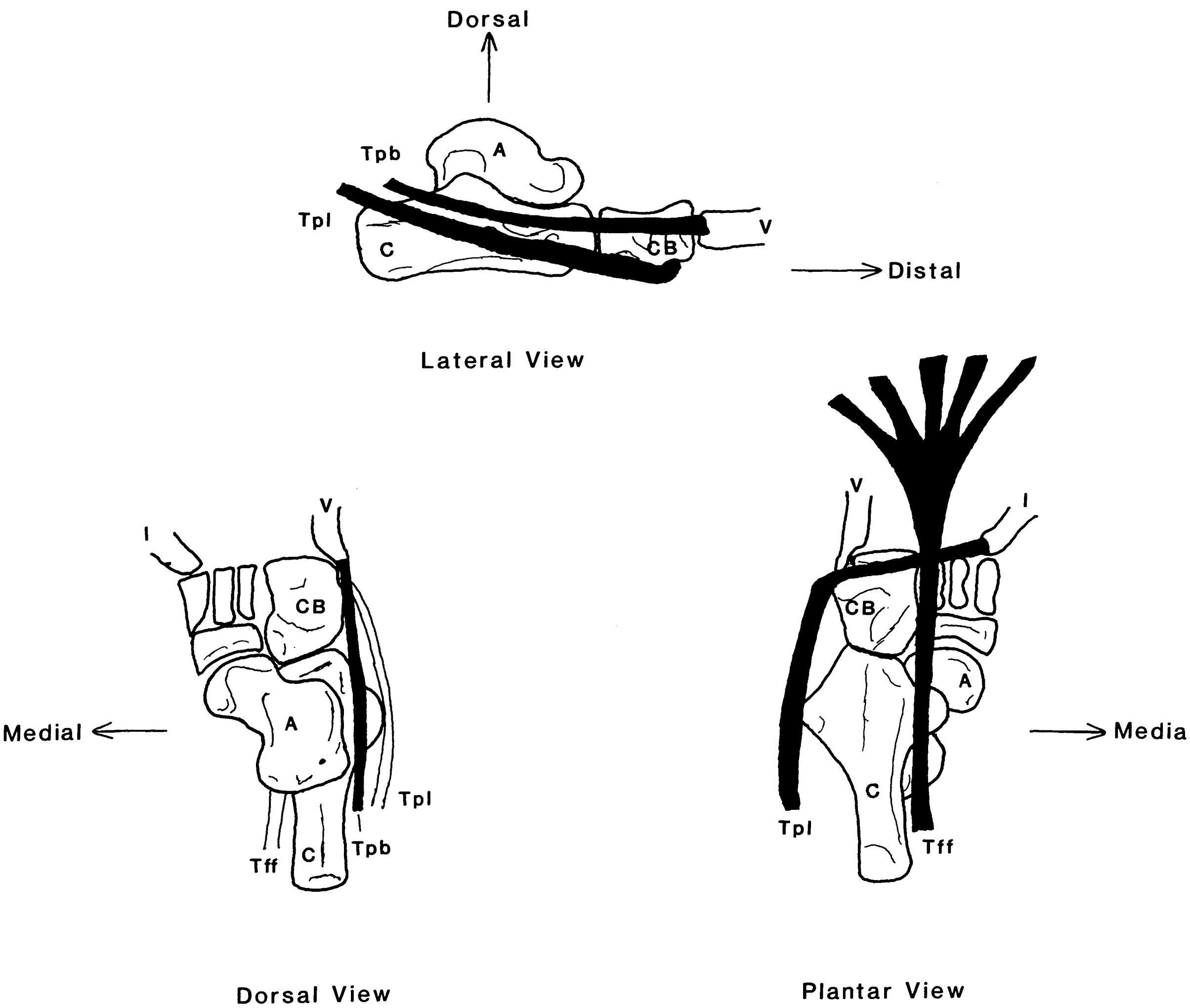

Figure 18. Course and insertion of some tendons of foot muscles. Top, lateral view showing course of tendons of peroneus longus and brevis along lateral side of foot; note insertion of peroneus brevis on lateral aspect of fifth metatarsal. Left, dorsal view of foot showing course of some foot tendons; note peroneus longus tendon wrapping around peroneal tubercle of calcaneum. Right, plantar view of foot showing course of some tendons of the foot; note that tendon of peroneus longus cuts across sole of foot to insert at base of first metatarsal. Abbreviations: A = astragalus, C = calcaneum, CB = cuboid, I = first metatarsal, V = fifth metatarsal, Tpb = tendon of peroneus brevis, Tpl = tendon of peroneus longus, Tff = tendon of flexor fibularis.

bution to more powerful plantar flexion of the foot. Such ability would be useful for a springing, climbing quadruped.

The evidence of the tarsal complex of archaic Paleocene plesiadapiforms is not very complete at this time. Szalay and Decker (1974) believe that it is complete enough to postulate that all plesiadapiforms were arboreal and should thus be included in primates (accepting arboreality as the Rubicon of "primateness"). What can be said is that the *Plesiadapis* foot was adapted for a number of diverse orientations, with inversion being a rather habitual posture. *Plesiadapis cookei* (based on UM 87990) was arboreal (Gunnell and Gingerich, in preparation), but was not a springer or leaper like euprimates. *P. cookei* was probably a slow climber that relied on large vertical supports.

Little evidence concerning other members of plesiadapiforms is, at present, available. Based on teeth, many of these taxa were exploiting habitats very different from those which *Plesiadapis* was presumably exploiting. Many of these taxa, including all microsyopoids and also carpolestid and plesiadapoids were probably exploiting dietary regimes much richer in insects than was *Plesiadapis*. Judging from their body sizes (all relatively small compared to *Plesiadapis*, except for some plesiolestines) and tooth mor-

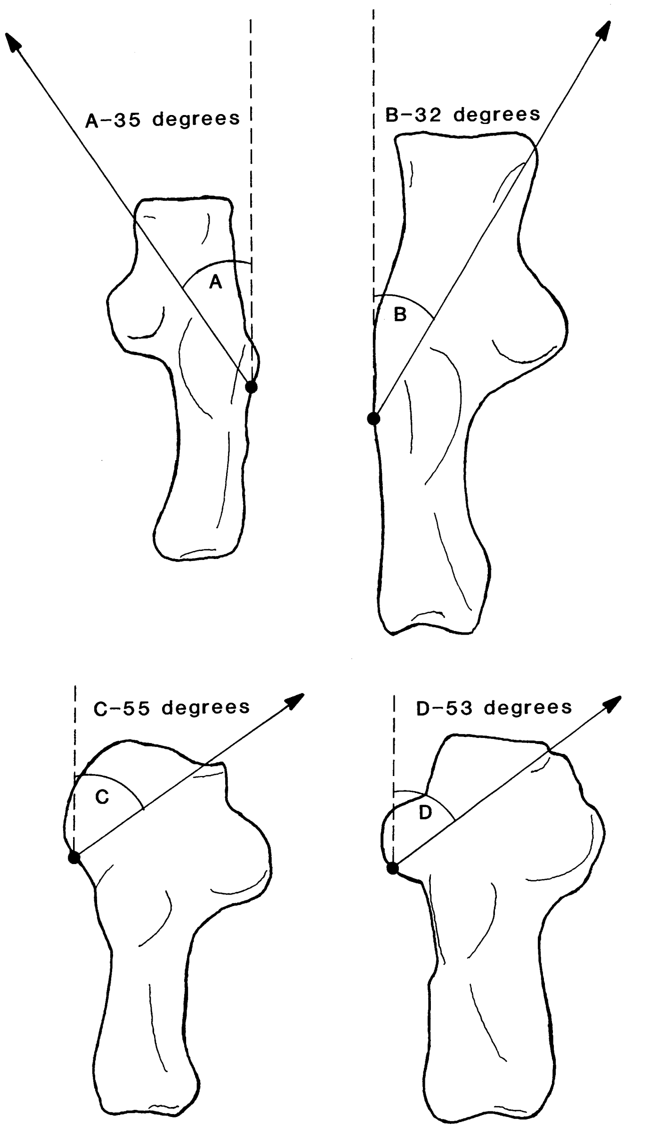

Figure 19. Force vectors for peroneus longus in *Adapis* (A), *Notharctus* (B), *Plesiadapis* (C), and *Marmota* (D). Closed circles represent insertion points of peroneus longus tendon on base of first metatarsal. Solid line connects insertion point with peroneal tubercle, which serves to orient the direction of applied force when peroneus longus contracts. Broken lines represent the long axis of the calcaneum from the peroneal tubercle. Arrows indicate force vector of peroneus longus. Angles represent quantification of these force vectors. An angle of 90 degrees would indicate that all of the force is applied laterally and would mean that the component of eversion is at its maximum, while an angle of 0 degrees would indicate that all of the force is applied proximally and would mean that the component of plantar flexion is at its maximum. *Adapis* and *Notharctus* have relatively lower angles than *Plesiadapis* and *Marmota*, indicating that plantar flexion is more important than eversion for peroneus longus in these adapids. The greater angles in *Plesiadapis* and *Marmota* indicate that the reverse is true in these taxa.

phology, it is possible that many were in a position to become visual predators. It is also likely that many were arboreal as well. As was noted above, *Plesiadapis* is specialized away from this insectivorous dietary regime and its postcranial anatomy is not likely to reflect that of other members of Plesiadapiformes. Many of these other taxa may well have been arboreal.

SUMMARY AND CONCLUSIONS

The above discussion of Paleocene plesiadapiforms has focused on three aspects of their morphology, dentition, cranial, and postcranial adaptations. The conclusions that can be drawn from the available evidence are not particularly satisfying. Dentally, the Paleocene radiation is very similar in cheek tooth morphology to primates of modern aspect that appear in the Eocene, but differ in anterior tooth morphology. There seems to be little doubt that many of the Paleocene taxa were exploiting dietary regimes similar to those exploited by the Eocene taxa, particularly those exploited by omomyid primates. Rather generalized tritubercular dentitions (with some variations, particularly in premolar morphology) typify most Paleocene taxa and early Eocene taxa, although adapids are slightly modified away from tritubercularity. Based solely on dental evidence, plesiadapiforms can be comfortably contained within the order Primates (although few if any of these dental attributes constitute shared and derived features between plesiadapiformes and euprimates).

Cranially, many of the features which have been used to exclude or include various taxa of archaic plesiadapiforms in the order are themselves of dubious value, due to their high variability in extant taxa which questions their taxonomic usefulness or to the difficulties in recognizing them in fossil forms. Much more evidence is required before meaningful taxonomic statements based on shared and derived character states can be attempted for most of the cranial aspects of these taxa. Generally speaking, based on relative brain sizes, long, low skull shapes, laterally facing orbits, and long snouts, plesiadapiforms appear to be at a "lower" level of organization compared to Eocene primates of modern aspect.

Postcranially, the evidence for plesiadapiforms is rather scant, but in *Plesiadapis* it suggests a rather mobile foot, capable of diverse orientations. It is likely, judging from postcranial evidence that *Plesiadapis* was a slow climbing arborealist. It is also likely that other plesiadapiform taxa may well have been arboreal. Small, insectivorous, arboreal animals were in a position to take advantage of the adaptations predicted by the visual predation hypothesis, and some of them may have already begun to exploit this dietary regime.

This returns us to the definition of primates and whether plesiadapiforms should be recognized as primates. Nearly every shared and derived feature that has been suggested in the past for the inclusion of some taxa and the exclusion of others of these archaic forms from the order Primates, has been shown to be either too variable or untestable in the fossil record, at least at the level of resolution now provided by the available evidence. If not variable or untestable, at the very best, convergence of character states cannot be ruled out in most cases.

MacPhee, Cartmill, and Gingerich (1983) advocate a gradistic approach to the recognition of primate-non-primate taxonomic boundaries. While unsatisfactory from the point of view of discrete, shared character states, it is more satisfactory from the point of view of reflecting the true state of our knowledge concerning the early differentiation and radiation of the order Primates. A Plesiadapiformes grade of organization is a discrete unit (albeit rather loosely defined at the bottom and top) which reflects the state of our knowledge concerning this group. Whether or not plesiadapiforms are included within primates or insectivores is perhaps less important than the recognition that a level of organization between insectivores and primates of modern aspect exists. The question should be rephrased to ask what plesiadapiforms can tell us about the differentiation and radiation of primate-like animals, not to ask whether they themselves should or should not be included in the order. Clearly most of the taxa included in plesiadapiforms are too derived to have been ancestral to any primates of modern aspect. Only *Purgatorius* is sufficiently primitive to have been representative of an ancestral form and there is little to suggest that euprimates share common ancestry with plesiadapiforms through a *Purgatorius*-like form. Plesiadapiforms can be included in primates only if they share a common ancestry with primates of modern aspect. Convincing evidence has not yet been produced to support a claim of common ancestry between plesiadapiforms and primates.

Not all plesiadapiforms failed to cross the boundary between the Paleocene and Eocene, the boundary that separates archaic mammals from their more modern counterparts. In the following three chapters I shall examine the evidence for the microsyopoid radiation in the late Paleocene and its survival and subsequent flourishing into and through the Eocene.

IV
HISTORY AND ORIGINS OF EOCENE MICROSYOPOIDEA

In the previous chapter the evidence pertaining to the Paleocene radiation of microsyopoid plesiadapiforms was examined. The Paleocene record is dominated by a few rich localities (see Chapter III) spread from New Mexico into Alberta. While some information can be gathered concerning overall patterns of evolution and the evolutionary relationships between plesiadapiforms in the Paleocene, little information concerning evolution within lineages can be gathered from the Paleocene record.

The situation is quite different in the Eocene. There are many localities that preserve plesiadapiforms. These localities are also spread from New Mexico into Canada, but within each regional area the localities are more plentiful than was the case in the Paleocene. While the best of the Paleocene localities are quarry sites where large concentrations of bone have been preserved, the Eocene localities are, for the most part, dominated by surface finds, making field prospecting much more profitable in the Eocene deposits. The advantages of rich surface localities are twofold. First, the numbers of specimens from a given locality are typically higher than at Paleocene localities (except at the richest quarry sites), so that a better understanding of ranges of variation for each sample is possible. More importantly, a series of surface localities can be arranged, one upon another, using stratigraphic superposition, allowing the direct application of a temporal component to the study of fossil material. With the use of stratigraphic superposition, morphological change through time can be directly studied. This is a great advance over the isolated Paleocene localities because it is possible to study species-level evolutionary changes in these Eocene deposits. Direct phylogenetic relationships can be inferred through the stratigraphic sequence.

The major disadvantage to a preponderance of surface finds is that these specimens are often less well preserved than those found in quarry settings. They are exposed to erosion upon being uncovered and are often fragmentary in nature, usually preserving only jaws and teeth.

Many areas in the North American Western Interior preserve badland topography that allows successive strata to be arranged in a stratigraphic sequence, giving a natural framework upon which to build phylogenetic sequences. By using the principles of faunal succession and correlation (see Chapter II), it is possible to correlate faunas in different areas and study similar phylogenetic sequences in these areas.

Of particular importance for this study is the Bighorn Basin in northwestern Wyoming. There, badland topography is preserved over hundreds of square miles. Measured stratigraphic sequences have been completed in three different areas within the Bighorn Basin (one in the Clark's Fork Basin, a northern extension of the Bighorn Basin, and two in the central Bighorn Basin) and these can be used to aid in constructing phylogenetic sequences for fossil mammals (see Gingerich and Gunnell, 1979; Gingerich and Simons, 1977, for some examples).

The purposes of this chapter are as follows. First, an historical perspective on Eocene plesiadapiforms and primates is presented, focusing primarily on microsyopids. A thorough understanding of the history of Eocene plesiadapiforms is critical for understanding the relationships between Paleocene and Eocene taxa. Second, the origin of Eocene microsyopids is discussed. Microsyopids are well represented in fossil assemblages from the Bighorn Basin and provide evidence concerning the origins of this family.

History of Eocene Plesiadapiformes

The first Eocene primates of modern aspect were found in Europe at the beginning of the 19th century. *Adapis* was first described by Georges Cuvier in 1812 and then named nine years later in 1821. *Adapis* has the distinction of being, not only the first Eocene primate named and described, but also of being the first fossil primate named (although Cuvier did not recognize it as such in 1821 as he felt it was similar to hyraxes and other artiodactyls).

The first North American Eocene fossil primate was not described until over forty years later. In 1869 Joseph Leidy described *Omomys carteri*, an omomyine tarsioid from the Bridger middle Eocene near Fort Bridger, Wyoming. As Cuvier before him, Leidy did not recognize *Omomys* as a primate, but instead thought it belonged to the hedgehog family Erinaceidae (Leidy, 1869). The following year Leidy (1870) described the adapid primate *Notharctus*, designating it as a carnivore similar to a raccoon. The two superfamilies of primates of modern aspect (Tarsioidea and Adapoidea) were described from North America by 1870.

Microsyopoids were first described shortly after this. The initial description of *Microsyops* has been the source of much confusion (Szalay, 1969b). In 1871, O.C. Marsh described a new species of the hyopsodontid condylarth

Hyopsodus, *H. gracilis* and a new genus *Limnotherium*, which he allied with *Hyopsodus*.

In April of 1872, Leidy (1872a), at a meeting of the Academy of Natural Sciences in Philadelphia, first proposed the name *Microsyops*. At that meeting he reported the finding (by Dr. J.V. Carter of Fort Bridger, Wyoming) of several lower jaw fragments of a "pachyderm" allied to *Hyopsodus*, from Grizzly Buttes (Bridger zone Br2 or Bridger B, see below and Chapter II). He believed that these jaw fragments were representative of the same animal "as that named *Hyopsodus gracilis* by Prof. Marsh." With this in mind, he proposed the new genus and species *Microsyops gracilis*, "which may be used in either case, whether the animal is or is not the same as *Hyopsodus gracilis*" (Leidy, 1872a). Leidy (1872b) formalized *Microsyops gracilis* in Hayden's fifth annual report to the U.S. Geological Survey, again noting his suspicion that Marsh's *Hyopsodus gracilis* was the same taxon. The type species of *Microsyops* was therefore *M. gracilis* (as of 1872).

In 1873, Leidy published his major work on the vertebrate fossils of the western territories in Hayden's 1873 report of the U.S. Geological Survey. It was in this report that the type species of *Microsyops* became confused. Leidy (1873, page 84) noted that the specific name *M. gracilis* was given to the original material because he felt that it was the same taxon as Marsh's *Hyopsodus gracilis*. However, since his original report Leidy had been shown a specimen of *H. gracilis* by Marsh and it was not the same as his *M. gracilis*, but his *M. gracilis* was the same as Marsh's species *Limnotherium elegans*. The type species of Marsh's genus *Limnotherium* was *L. tyrannus*, which is generically distinct from *Microsyops*, therefore *Microsyops* remained a valid genus with *L. elegans* as a species. Leidy noted that the proper name for the type species of *Microsyops* should be *M. elegans*, not *M. gracilis*, as *Limnotherium elegans* had chronological priority over *Hyopsodus gracilis*.

In 1881 Cope named two new species of *Microsyops* from the Wind River Basin, *M. speirianus* and *M. scottianus*, and also noted the presence of Leidy's *M. gracilis* (Cope apparently either ignored or was unaware of Leidy's change of *M. gracilis* to *M. elegans*).

Cope (1882) named a new genus and species of microsyopid, *Cynodontomys latidens* from the "Wahsatch" beds of the Bighorn Basin. Cope (1882) noted that the teeth of *Cynodontomys* resembled those of *Anaptomorphus* (an Eocene tarsioid from North America) and *Necrolemur* (an Eocene tarsioid from Europe). He included *Cynodontomys* in his suborder Prosimiae along with *Anaptomorphus*.

Cope (1883a) named *Mixodectes pungens* from the Puerco Eocene (now the Torrejonian, middle Paleocene) of New Mexico. He was unable to place this taxon within any higher taxonomic group but did note that it was similar to *Pelycodus* and *Cynodontomys*, placed in the suborders Mesodonta and Prosimiae, respectively. He also named a second species of *Mixodectes*, *M. crassiusculus* in the same paper (Cope, 1883a).

Cope (1883c) named a new genus and species, *Indrodon malaris*, and put it in Anaptomorphidae. Anaptomorphids (characterized by two upper premolars) and mixodectids (characterized by three upper premolars) were now included within Prosimiae in the superfamily Lemuroidea.

In later 1884 (Cope, 1884b), Cope's major work on vertebrates from the western territories was published in the Report of the U.S. Geological Survey of the Territories for 1884. In this report Cope further defined and refined his order Bunotheria. Bunotheres were characterized by the following: 1) cerebrum small leaving olfactory bulbs exposed and with cerebral hemispheres smooth; 2) ambulatory limbs with varying numbers of compressed ungues; 3) transverse glenoid articulation; 4) upper molars tubercular, lacking continuous crests (lower molars often similar); 5) incisors present in premaxilla; 6) all teeth invested with enamel; 7) normally possessing five digits; 8) and femur normally possessing a third trochanter.

Cope included within the order Bunotheria the suborders Creodonta, Mesodonta, Insectivora, Tillodonta, Taeniodonta, and perhaps Prosimiae. He noted that Mesodonta and Prosimiae may well be rather closely related. Mesodonts were distinguished by non-ever growing incisors, tubercular molars (never sectoral), elevated third trochanters on femurs, and an ungrooved astragalar trochlea.

Cope distinguished Prosimiae from Mesodonta by the possession of an opposable hallux in the former suborder. He noted that many of the genera included in Mesodonta and Prosimiae were unknown postcranially and may have conceivably belonged to different suborders (he moved *Microsyops* and *Anaptomorphus* from Mesodonta to Prosimiae in a footnote to page 240, in his 1884b publication). Within Prosimiae Cope recognized three families, Adapidae (with four premolars), Mixodectidae (with three premolars), and Anaptomorphidae (with two premolars).

Osborn and Wortman (1892) described some of the American Museum's 1891 collection from the Wasatch and Wind River beds (Eocene) of Wyoming, gathered principally by Wortman. They moved many of Cope's Mesodonta genera to the order Primates. They included one family in the suborder Lemuroidea, Anaptomorphidae; three other families, Adapidae, Notharctidae, and Microsyopsidae (now generally referred to as Microsyopidae) they tentatively placed in the suborder Anthropoidea, arguing that these families bear the same relationship to modern anthropoids that Eocene perissodactyls bear to modern Perissodactyla.

Osborn and Earle (1895) described American Museum collections from the San Juan Basin, New Mexico, collected in 1892. They included two families in the order Primates, Anaptomorphidae and Mixodectidae. *Indrodon malaris* was the only anaptomorphid recognized from New

Mexico, while two species of *Mixodectes* (*M. pungens* and *M. crassiusculus*) were included in mixodectids. A third family, Chriacidae, was also included in primates.

Matthew (1897) published his first revision of the New Mexican Puerco fauna two years later. As did previous authors, Matthew recognized two faunal levels in the Puercan, an upper and lower level. However, he also noted that there was no faunal overlap between these two levels and that two distinct faunal horizons should be recognized. The upper, thin layer was given a new name, the Torrejon horizon, while the lower beds (two different horizons, but not faunally distinct from one another) were retained in the Puerco horizon. Matthew further noted that neither of these two horizons shared any taxa in common with Wasatchian forms, nor were there any clearly recognizable ancestor-descendant relationships between either the Puerco or the Torrejon and the Wasatchian faunas. This, combined with the primitive, unspecialized nature of the Puerco and Torrejon faunas led Matthew to the conclusion that they were older than the Wasatchian faunas and he considered both New Mexican horizons to represent a basal Eocene age.

Matthew (1897) recognized no primates from the Puercan. *Indrodon malaris* (from the Torrejonian) was questionably put in Anaptomorphidae based on the skeletons assigned to this species by Osborn and Earle (1895). Matthew noted the dental similarities between *Indrodon* and *Mixodectes*. He moved the two *Mixodectes* species (*M. pungens* and *M. crassiusculus*) to the Rodentia and noted that *Microsyops* may belong there as well, but he questioned any close relationship between *Microsyops* and mixodectids. The rodent characters Matthew recognized in *Mixodectes* were based on the partial skeleton associated with a *Mixodectes* specimen, particularly an astragalus that he felt was similar to *Plesiarctomys* (a middle and upper Eocene paramyid rodent from Europe).

In 1899, Matthew again maintained this position (Matthew, 1899) of keeping mixodectids in Rodentia. He also retained *Indrodon malaris* in primates in the family Tarsiidae. He included the Wasatchian forms *Microsyops* and *Cynodontomys* in primates, as well.

Osborn (1902) reviewed the relationship between Rodentia and Mixodectidae, and attempted to clarify the relationship of many of the mixodectid and microsyopid species that Cope, Marsh, and others had named during the late 19th century. Osborn recognized no primates in the "basal Eocene" Puercan and Torrejonian horizons. He recognized three families in the Wasatchian as representative of Primates: Hyopsodontidae, Notharctidae, and Anaptomorphidae.

Jacob Wortman (1903–1904) published his study on the primates in the Marsh collection in the Peabody Museum at Yale University. Wortman rejected Matthew's and Osborn's ideas of rodent affinities for mixodectids and microsyopids. He noted first that it was very unlikely that the astragalus that Matthew had described as that of *Mixodectes* was associated with the dental fragments supposedly associated with it. Second, he felt that the characteristics of the molars argued for a closer relationship to adapid primates than to rodents. Finally, he felt that the specializations of the anterior dentition (enlarged upper and lower central incisor, loss of lateral incisors) were not representative of rodent affinities, but were very similar to those found in *Cheiromys* (or *Daubentonia*), the Malagasy aye-aye.

Matthew (1909a) reviewed the relationships of many insectivore and carnivore species from the Bridgerian Land-Mammal age, middle Eocene. This paper represented the beginning of Matthew's doubts as to the rodent affinities of mixodectids and microsyopids (he separated the two families here and questioned whether they are closely related). Matthew suggested that mixodectids may be more closely related to insectivores than to rodents.

Later in the same year, Matthew (1909b) formalized these conclusions by moving microsyopids (*Cynodontomys* and *Microsyops*) into primates and mixodectids (*Mixodectes* and *Indrodon*) to Insectivora. He noted the possibility that microsyopids might be insectivores and that mixodectids might be rodents, but was quite sure that these possibilities were rather unlikely.

In 1915 Matthew and Granger published their revision of the Wasatch and Wind River faunas. In his section on primates and insectivores Matthew (1915) altered his position from 1909, but only slightly. Matthew retained Mixodectidae in Insectivora, but noted that these taxa have many dental similarities to primates. Again Matthew stressed that microsyopines may not be closely related to mixodectines and felt that it was possible that they (microsyopines) were tarsiids.

Matthew (1937) finalized his ideas concerning mixodectids in his last revision of the Puerco faunas, published posthumously under the editorship of Walter Granger, William King Gregory, and Edwin H. Colbert. Matthew noted the difficulty in defining an order Insectivora and even suggested that perhaps it should be divided into six or seven separate orders (including Chrysochloroidea, Centetoidea, Soricoidea, Erinaceoidea, Pantolestoidea, Menotyphla, and an additional order for Mongolian Cretaceous insectivores). Matthew suggested that mixodectids, plesiadapids, macroscelidids, and tupaiids should all perhaps be included within menotyphlans, recognizing the difficulties in classifying those families. However, Matthew (1937) retained the order Insectivora and recognized four Paleocene (by now the Puercan, Torrejonian, and Tiffanian had been grouped together in the Paleocene epoch) insectivore families, Leptictidae, Pantolestidae, Palaeoryctidae, and Mixodectidae.

To this point it becomes apparent how the history of the two families most relevant to this chapter, Mixodectidae and Microsyopidae, had become intertwined. After the original description of *Microsyops* (by Leidy and Marsh) from the middle Eocene Bridgerian of Wyoming in the 1870's, Cope described *Mixodectes* from the Puerco of the San Juan Basin, New Mexico. Believing that these faunas were nearly contemporaneous, he linked *Mixodectes* and *Microsyops*, based solely on the lower dentitions, which are quite similar in detail. The original linking of these two genera influenced most later work up to the time when Matthew first raised the possibility that these forms may not be truly related, and continued to affect workers even beyond this point.

Simpson (1927) described a fauna from the Paskapoo Formation in Alberta, Canada. In this paper he described a new genus and species, *Elpidophorus elegans*, which, at that time, he felt was either an insectivore or a carnivore, including it tentatively in the latter order as an oxyclaenid (a family now synonymized with arctocyonid condylarths). In 1935, Simpson published his initial report on Paleocene mammals from the Fort Union Formation in Montana, describing among other forms, a new mixodectid, *Eudaemonema cuspidata*. He noted that *Eudaemonema* was so distinctive that it may not belong to this family, but that, "it compares more nearly with *Mixodectes*, *Cynodontomys*, and their respective allies than with other genera known to me." Simpson noted that the P_4 structure was similar to *Cynodontomys*, while the molars were more reminiscent of *Mixodectes*.

Simpson (1936a) listed *Mixodectes*, *Indrodon*, and *Eudaemonema* as mixodectids in the order.Insectivora. Later in that year (Simpson, 1936b) he described the fauna from Scarritt Quarry, Fort Union Formation of Montana (early late Paleocene). In this paper he named a new species of *Elpidophorus*, *E. patratus*, as a mixodectid insectivore (moving *Elpidophorus* from his 1927 designation as an oxyclaenid). Simpson noted the relative complexity of upper P3 in this species, stating that it was similar to a P^4 described by Matthew (1915) as that of *Cynodontomys angustidens*. Simpson felt that Matthew had misidentified this *Cynodontomys* specimen and instead of being P^4-M^1 as Matthew had said, Simpson felt that this specimen probably represented P^{3-4} (as we shall see below, Matthew was correct in his identification). With this new interpretation of the *Cynodontomys* specimen, Simpson went on to note the similarities between it and *Elpidophorus patratus*. He felt that these taxa were closely related. He continued to retain *Cynodontomys* and *Microsyops* in mixodectids, and retained mixodectids in Insectivora, even though he noted that they had very few insectivore characteristics. Simpson noted that Insectivora continued to serve as a "scrap basket" order for a number of unspecialized early families.

In 1937, Simpson published his major monograph on the Fort Union fauna of the Crazy Mountain Field in Montana. In this paper, Simpson (1937a) put mixodectids in Insectivora. Simpson included *Eudaemonema* in mixodectids because it bridges the morphological gap between *Mixodectes* and *Microsyops*. Thus he too was influenced by the initial tying together of these genera by Cope.

Simpson (1937a) also noted the possibility that mixodectids (in particular *Elpidophorus* and *Eudaemonema*) may be related to plagiomenid dermopterans. Among the features shared by some mixodectids and dermopterans, Simpson noted the following: 1) a molarized P_4; 2) upper molars with a strong transverse valley; 3) small hypocones (only in *Elpidophorus*); 4) wide stylar shelves with a tendency towards the addition of accessory cuspules; 5) internal lower cusps elevated on P_4 and molars; 6) metaconid and entoconid opposite or anterior to the protoconid and hypoconid respectively; 7) paraconids and trigonids generally similar; 8) and molar talonids broadened. Simpson rejected a close relationship between plagiomenids and mixodectids because plagiomenids have a double mesostyle lacking in mixodectids, retain lateral incisors and do not have enlarged central incisors, do not have hypoconulids displaced lingually, and have deep cheek teeth with cusp proliferation that is lacking in mixodectids.

In 1941, C. Lewis Gazin described the Paleocene faunas from Dragon Canyon and North Horn Mountain, in Utah. Among the taxa from Dragon Canyon (Dragonian, early Paleocene) was a new mixodectid named and described by Gazin as *Dracontolestes aphantus*. Gazin included mixodectids in insectivores.

Simpson published his mammalian classification in 1945. In it he classified mixodectids as insectivores in the new superfamily Mixodectoidea (= Mixodectoidae of Hay, 1930). Saban (1954) followed Simpson's classification, only differing by placing the superfamily Mixodectoidea within its own suborder Mixodectomorpha. McKenna (1955a,b) also placed mixodectids in insectivores. McKenna (1960a) suggested that perhaps *Eudaemonema* was not a mixodectid, but may be a tupaioid instead. The other mixodectids (as defined by Simpson, 1945) McKenna included in insectivores in the suborder Menotyphla.

Later in 1960, McKenna (1960b) published a monograph on the fossil mammals from the Wasatchian Four Mile Fauna in Colorado. Among other taxa described by McKenna, there was a new species of *Cynodontomys*, *C. alfi*. McKenna felt that it was the earliest microsyopid from the Eocene and he noted that the upper fourth premolar was not molariform, as were later *Cynodontomys* and *Microsyops*, but was distinctly premolariform. As it turns out, McKenna misidentified this tooth, but this did not affect his reasoning; see below. If this was true, then *Eudaemonema* was not intermediate between *Mixodectes* and primitive microsyopids, as Simpson (1937) had suggested. This led McKenna to remove *Eudaemonema* from mixodectids and place it very questionably in tupaioids. McKenna (1960b) removed *Elpidophorus* from mixodectids and put it in Plesiadapidae, *incertae sedis*. He also moved microsyopids into primates. This left only

Mixodectes, *Dracontolestes*, and *Olbodotes* in mixodectids. McKenna (1966) also followed this interpretation, keeping microsyopids in primates and mixodectids in insectivores, but noting that the latter were probably close to the ancestry of primates.

Van Valen (1967) reviewed a number of insectivore families and the relationships among insectivores. In this paper he linked mixodectids and dermopterans. He placed mixodectids in the suborder Dermoptera, superfamily Mixodectoidea, within the order Insectivora. The other dermopterans he placed in the superfamily Galeopithecoidea, in two families, Plagiomenidae (including the fossil forms *Plagiomene*, *Planetetherium*, and *Thylacoelurus*) and Galeopithecidae (including the living forms *Galeopithecus* (=*Cynocephalus*) and *Galeopterus*. Microsyopids are retained in Prosimii by Van Valen (1967, 1969). Both D.E. Russell (1967) and L.S. Russell (1967) retained mixodectids in Insectivora as distinct families, not related to plagiomenids, while Sloan (1969) concurred with Van Valen (1967) by putting mixodectids in Dermoptera.

In 1969, Szalay published a major revision and study of mixodectids and microsyopids. He followed Russell (1964, 1967) in putting mixodectids in Insectivora, in their own superfamily Mixodectoidea. He rejected any relationship with plagiomenids for any of the mixodectid genera. Szalay (1969b) retained Microsyopidae in primates of uncertain suborder following McKenna (1960b, 1966), although McKenna (1967) removed microsyopids from primates.

Szalay (1969a) also published, in the same year as his mixodectid-microsyopid revision, another paper in which he added a new subfamily, Uintasoricinae, to microsyopids. Matthew (1909a) had named the tiny genus *Uintasorex*, provisionally placing it in the suborder Proglires along with mixodectids and microsyopids, but in a new family, Apatemyidae. Since Matthew's initial description of *Uintasorex*, it has been shuffled from one group to another, including Apatemyidae (Matthew, 1915, 1917b; Matthew, Gregory, and Mosenthal, 1910), Plesiadapidae (Abel, 1931; Scholosser, 1923), Chiromyidae (Teilhard, 1922), Anaptomorphidae (Gazin, 1958; Robinson, 1966, 1968; Simons, 1963; Simpson, 1940, 1959), and Primates, *incertae sedis* (Simpson, 1945).

By 1971, Szalay had changed his position. Szalay (1971, 1972) removed microsyopids from primates and united paromomyids, picrodontids, plesiadapids, and carpolestids in the superfamily Plesiadapoidea. Szalay (1972) pointed out that his concept of Plesiadapoidea was similar to Van Valen's (1969) concept of Microsyopoidea with microsyopids removed and restricted to the Eocene radiation (a position also supported by McKenna, 1966). In 1973, Szalay raised plesiadapoids to subordinal rank, naming the new suborder Paromomyiformes. Szalay (1973) stated that he chose the name Paromomyiformes because of his belief that paromomyids reflect the most primitive characteristics attributable to the suborder.

Other authors who continued to recognize microsyopids as primates included Guthrie (1971), Gazin (1976), Bown and Gingerich (1972), Golz and Lillegraven (1977) and Lillegraven (1976). In 1973 Bown and Gingerich discussed the origins of Eocene microsyopids, concluding that Paleocene paromomyids were likely ancestors of microsyopids, therefore solidifying the position of microsyopids in primates. Bown and Rose (1976) continued to support this position, moving Microsyopidae out of Plesiadapoidea to uncertain superfamily position within Primates. Gingerich (1976) put the family Microsyopidae in the superfamily Microsyopoidea, including the subfamilies Microsyopinae, Uintasoricinae, and Purgatoriinae. Paromomyids were moved to the superfamily Plesiadapoidea by Gingerich.

Since 1976, most authors have agreed on the split between mixodectids and microsyopids, with mixodectids being included in insectivores and microsyopids being included in either insectivores, as a family distinct and distantly related to mixodectids, or included in primates (see Wolberg, 1979; Rigby, 1980; Russell, 1981; Rose and Bown, 1982; Bown, 1982; Lucas, 1982; Kihm, 1984; Gunnell and Gingerich, 1981; Rudman, 1981; Gunnell, 1985; Szalay, 1977; Szalay and Delson, 1979; Schwartz and Krishtalka, 1978; Krishtalka, 1978; Schwartz, Tattersall, and Eldredge, 1978; Simons, 1972; Rose, 1981a; and Eaton, 1982). Rose (1975b) suggested that *Elpidophorus*, instead of being a mixodectid, belongs in Dermoptera, leaving only *Dracontolestes*, *Mixodectes*, *Eudaemonema*, and *Remiculus* in mixodectids.

Microsyopids are now constituted by two subfamilies, Microsyopinae and Uintasoricinae (although Krishtalka, 1978, Schwartz and Krishtalka, 1978, and Schwartz, Tattersall, and Eldredge, 1978 put uintasoricines in tarsiiforms as a family Uintasoricinae). Microsyopines are represented by the Eocene genera *Microsyops*, *Arctodontomys* (Gunnell, 1985), and *Craseops*. Uintasoricines are represented in the Eocene by *Uintasorex* and *Niptomomys* and in the Paleocene by *Navajovius*, *Berruvius*, and possibly *Palenochtha*. The latter three genera have often been allocated elsewhere, as have *Tinimomys* and *Micromomys*; these two genera are also included in microsyopids by some authors.

EOCENE MICROSYOPID ORIGINS

As is seen from the discussion of the history of the taxonomic relationships of microsyopids, it is difficult to define the origins of this group. Three possible points of origin for the Eocene microsyopid group are: 1) Paleocene mixodectids; 2) palaechthonid plesiadapiforms; 3) leptictid insectivores (see Szalay, 1972). Within microsyopids, it is necessary to examine the origins of microsyopines and uintasoricines separately, as it is possible that each of these subfamily groups arose from distinctly different ancestral stocks and may not be as closely related as grouping them together in Microsyopidae suggests. To assess the probability of origination of microsyopids from any one of the three possibilities listed above, each group of possible ancestors will have to be examined in detail, with respect to both microsyopines and uintasoricines. In this section, each of the groups is examined successively in an attempt to ascertain the relationship of each to microsyopids.

MIXODECTIDAE

As was discussed above, mixodectids were first described by Cope (1883b) with the naming and description of two species of *Mixodectes*, *M. pungens* and *M. crassiusculus*, which Cope noted were similar to *Cynodontomys* in the pattern of their molar morphology. Other members of the family as recognized by Szalay (1969b) were added in subsequent years, including *Indrodon malaris* (Cope, 1883c), now placed in *Mixodectes*, *Elpidophorus elegans* (Simpson, 1927), *Elpidophorus minor* (Simpson, 1937a), *Eudaemonema cuspidata* (Simpson, 1935), *Dracontolestes aphantus* (Gazin, 1941), and *Remiculus deutschi* (Russell, 1964). Since that time Rose (1975b) has removed *Elpidophorus* from mixodectids and placed it in Plagiomenidae within the order Dermoptera. The following revision is provided after careful study of most of the relevant specimens, either as original material or epoxy casts, or in the case of *Remiculus*, as stereo photographs.

SYSTEMATICS OF MIXODECTIDAE

Order INSECTIVORA Bowdich, 1821
Superfamily Mixodectoidea Simpson, 1945
Family Mixodectidae Cope, 1883

Type Genus.—Mixodectes.

Included Genera.—Mixodectes, Dracontolestes.

Age and Distribution.—Torrejonian, middle Paleocene, from northwestern New Mexico, central Utah, and southernmost, west-central Wyoming.

Emended Diagnosis.—Mixodectids can be characterized as follows: 1) retention of a primitive premolariform P_3; 2) the presence of a premolariform, often enlarged P_4, with a tiny to absent paraconid and an absent metaconid; 3) oblique cristid which joins the postvallid of the molar trigonids buccally; 4) molar hypoflexids steeply angled and not extended buccally; 5) weak to developed upper molar paraconules, somewhat shelf-like where developed, and weak to absent metaconules, never shelf-like; 6) preparaconule cristae fairly strong and often join parastylar region, while postparaconule cristae and metaconule cristae are weak to absent; 7) upper molar hypocones strong, but joined to the posterior flank of the protocone; 8) upper anterior molar cingula present to weak, posterior cingula weak to absent, never joined lingually; 9) P^4 premolariform with no metacone, conules, or transverse valley; 10) and loss of lower and upper canines (or upper and lower I2), and loss of upper and lower P1.

Discussion.—In his diagnosis, Szalay (1969b) noted that mixodectids possessed long and wide paracristae and metacristae. While this is true for some genera included in mixodectids by Szalay (for example *Eudaemonema* and *Elpidophorus*) it is certainly not true for *Mixodectes* itself. Szalay stated that the presence of enlarged upper and lower incisors (I1) was diagnostic of the family, a trait that remains unknown in *Dracontolestes*, *Elpidophorus* (with the possible exception of I^1, see Szalay, 1969b, page 220), and *Remiculus*.

McKenna (1960a) noted that mixodectids fall into three morphological groupings, *Mixodectes* and *Dracontolestes*; *Cynodontomys*, *Microsyops*, and *Craseops*; and *Elpidophorus* and *Eudaemonema*. He removed the *Microsyops*, *Cynodontomys*, *Craseops* triad from mixodectids, and put *Eudaemonema* in tupaioids, *incertae sedis*, and *Elpidophorus* in ?Plesiadapidae, *incertae sedis*. While disagreeing with the assignment of the last two genera, I do agree that their inclusion within mixodectids is not warranted either (nor is this warranted for *Remiculus*). In assessing the affinities of these genera, Szalay (1969b) stressed the similarities and apparent dominance of dental shearing mechanisms in these genera. A shearing dominated dentition is the case for these genera, but the morphological attributes which contribute to these masticatory systems are different. *Eudaemonema* and *Remiculus* each have a set of derived characteristics different from that shared by *Mixodectes* and *Dracontolestes* (see below). This argues for a more distant relationship between the former and latter two genera.

Dracontolestes Gazin, 1941

Dracontolestes Gazin, 1941, p. 13; Szalay, 1969b, p. 228; Tomida, 1981, p. 237.

Type Species.—Dracontolestes aphantus.

Included Species.—Type only.

Age and Distribution.—Dragonian, early-middle Paleocene (To1), Emery County, Utah.

Diagnosis.—Differs from *Mixodectes* in having a more centrally placed hypoconulid on M_3, by having the entoconid only slightly taller or equal in height to the hypoconid, in having molar talonids strongly closed off lingually, and in being smaller.

Dracontolestes aphantus Gazin, 1941

Dracontolestes aphantus Gazin, 1941, p. 13, fig. 6; Szalay, 1969b, p. 228, Pl. 23, figs. 1–4; Tomida, 1981, p. 237.

Holotype.—USNM 16180, left mandible with M_2 talonid and M_3.

Horizon and Locality.—NW1/4, S8, T19S, R6E, Emery

County, Utah, in the Joes Valley Member of the North Horn Formation.

Hypodigm.—The type specimen and USNM 15719, a left mandible with an M_2 talonid.

Diagnosis.—As for genus.

Discussion.—*Dracontolestes* remains very poorly known. The two specimens were described in 1939 and 1941 and no new material has been found since the initial discoveries. The M_2 talonids have entoconids and hypoconids of equal size and height and a low, slightly lingually placed hypoconulid. The talonid basin is quite broad and deep and is closed off lingually by a fairly strong entocristid. There is an indication of a very weak mesoconid and there is no posterior cingulid. All of these feature are shared with one or the other or both *Mixodectes* species.

M_3 is similar in most details to *Mixodectes* as well. The metaconid is rather tall and bulbous, slightly taller than the protoconid. The paraconid is shelf-like, but is sharply defined. The entoconid and hypoconid are subequal in height with a sharp, rather gracile entoconid and a more bulbous hypoconid. The talonid, as in M_2, is closed off lingually by a strong entocristid, more strongly developed than in *Mixodectes*. The hypoconulid is large and positioned almost centrally on the posterior aspect of the tooth. It is separated from the entoconid by a deep V-shaped notch, better defined than in *Mixodectes*. There are no cingulids on M_3. The talonid basin is rather deep, as in M_2 and as in *Mixodectes*.

Dracontolestes differs from *Mixodectes* in only a few minor ways, but it is poorly known and from a presumably earlier horizon so that I believe the generic distinction should be maintained, pending further fossil evidence. There is little doubt that if not congeneric, *Dracontolestes* and *Mixodectes* are very closely related.

Mixodectes Cope, 1883

Mixodectes Cope, 1883a, p. 30; 1884b, p. 240; Osborn and Earle, 1895, p.7; Matthew, 1897, p. 265; Matthew, 1899, p. 29; Osborn, 1902, p. 203; Wortman, 1903–1904, p. 203; Matthew, 1909a, p. 546; Matthew, 1937, p. 220; Simpson, 1936a, p. 3; Matthew, 1915, p. 466; Simpson, 1937a, p. 127; Simpson, 1945, p. 53; McKenna, 1960b, p. 76; Van Valen, 1967, p. 261; Szalay, 1969b, p. 211; Taylor, 1981, p. 258; Tsentas, 1981, p. 271.

Indrodon Cope, 1883c, p. 318; Osborn and Earle, 1895, p. 7; Matthew, 1897, p. 265; Matthew, 1899, p. 29; Osborn, 1902, p. 208; Simpson, 1936a, p. 3; Matthew, 1915, p. 466; Simpson, 1937a, p. 127; Simpson, 1945, p. 53.

Olbodotes Osborn, 1902, p. 205; Wortman, 1903–1904, p. 203; Matthew, 1909a, p. 547; Matthew, 1915, p. 467;

Oldobotes, McKenna, 1960b, p. 76.

Type Species.—*Mixodectes pungens.*

Included Species.—Type species and *Mixodectes malaris.*

Age and Distribution.—Torrejonian, middle Paleocene of northwestern New Mexico and southernmost, west-central Wyoming.

Diagnosis.—See generic diagnosis for *Dracontolestes.*

Mixodectes pungens Cope, 1883

Mixodectes pungens Cope, 1883a, p. 559; Cope, 1884b, p. 241, Pl. 24f, fig. 1; Cope, 1885, p. 465, fig. 9; Osborn and Earle, 1895, p. 7; Matthew, 1897, p. 266, fig. 1; Matthew, 1899, p. 29; Matthew, 1909a, p. 546; Osborn, 1902, p. 206, figs. 30–31; Matthew, 1937, p. 221, Pl. 57, figs. 3,6; Szalay, 1969b, p. 213, Pl. 17, figs. 1–4, Pl. 18, figs. 1–4, Pl. 19, figs. 1–6, Pl.20, figs. 1–5, Pl. 21, figs. 1–3; Tsentas, 1981, p. 271.

Mixodectes crassiusculus Cope, 1883a, p. 560; Cope, 1884b, p. 242, Pl. 24, fig. 2; Osborn and Earle, 1895, p. 7; Matthew, 1899, p. 29; Osborn, 1902, p. 207, fig. 32; Matthew, 1937, p.222, Pl. 57, figs. 1–2.

Olbodotes copei Osborn, 1902, p. 205, fig. 29.

Holotype.—AMNH 3081, right mandible with roots for $I_{1\text{-}2}$, alveolus for P_2, and broken P_3-M_3, found by David Baldwin in the vicinity of Kimbetoh Village, San Juan Basin, New Mexico (see Simpson, 1948, 1959, and 1981).

Age and Distribution. — *Pantolambda/Plesiadapis praecursor* Interval-Zone (To3), Torrejonian, middle Paleocene, of San Juan Basin, New Mexico.

Diagnosis.—Differs from *Mixodectes malaris* by being larger, by having relatively larger upper and lower fourth premolars, by having stronger mesoconids, by having a better developed transverse valley on upper molars, by having weaker paraconules on upper molars, by lacking or having a weak anterior cingulum on upper molars, and by having a weak stylocone.

Discussion.—Szalay (1969b) indicated that *M. pungens* was represented in *Pantolambda* Zone Torrejonian levels, while *M. malaris* was present only in *Deltatherium* Zone levels (Torrejonian zone To2). Recently Tsentas (1981) has reported the finding of both species at the same localities within the *Pantolambda* Zone. Neither Szalay (1969b) nor Tsentas (1981) recognize any morphological differences between these two species (Tsentas notes that with the collections recently made by New York and Brown Universities, it should be possible to see if size differences warrant specific separation). After examining a number of specimens, I find sufficient differences to warrant a specific separation.

Mixodectes pungens has a robust I_1 root that is distinctly laterally compressed, as is the root of I_2, which is positioned closely behind the root of I_1. In *Mixodectes malaris*, I_1 is enlarged but not as much relative to I_2 as in *M. pungens*. I_1 is slightly laterally compressed, while I_2 has a more triangular root than is the case in *M. pungens*. As in *M. pungens*, I_1 and I_2 are crowded together forming a functional incisor field. In both species a small single-rooted tooth follows I_2, interpreted by Szalay (1969b) as P_2, which is probably correct. P_3 is double rooted in both species, P_3 in *M. pungens* is often oriented slightly obliquely in the mandible (anterior-lingually to posterior-buccally) and has a better developed talonid heel.

P_4 is similar in both species, but there are subtle differences. In *M. pungens*, P_4 is very large, relatively larger than in *M. malaris* (although it is quite large in *Mixodectes malaris*, as well). On the anterior flank of the protoconid is a small but distinct paracristid, although neither species possesses a paraconid. *M. pungens* often may exhibit a small cuspule or enamel fold in the position of the paraconid. In some specimens of *M. pungens*, the paracristid is very weak. Neither species has a metaconid on P_4. The P_4 talonid in *M. pungens* is often well developed, but very low and lacking relief. It usually has a weak hypoconid and a fairly well developed posterior-lingual cristid with a tiny entoconid cuspule variably developed. The talonid slopes gently away buccally and is flattened lingually. The talonid of P_4 in *M. malaris* is similarly positioned very low on the posterior aspect of the tooth. It normally possesses a single, centrally placed cusp with a weak lingual cristid running from this cusp to the lingual base of the protoconid. The talonid slopes rather abruptly away, both buccally and lingually from the central cusp in most cases, while the lingual side may be less steeply sloping and flatter (as in *M. pungens*) in a few cases.

The lower molars are very similar in both species, differing only in the stronger development of a mesoconid in *M. pungens*. The upper premolars are very poorly known, but appear to be similar in both species. The upper molars are also similar but some difference do exist. Both species have a prominent protocone, metacone, and paracone, with the protocone slightly lower than the other two cusps. In *M. pungens*, the trigon basin is more open and flattened lingually, while in *M. malaris* it is often more closed and steeply angled due to a relatively taller, less lingually displaced protocone. The protocone is centrally placed directly opposite the mesostyle in both species (or slightly anterior). Both species have a large, bulbous hypocone that arises from the posterior flank of the protocone (that is, not separated by a cleft or V-shaped crevice, from the protocone). Both species have a transverse valley that separates the upper molars into anterior and posterior segments, giving the teeth a distinct dilambdodont character. This transverse valley is less distinct on M^3 in both species and may be slightly weaker on M^{1-2} in *M. malaris*. Both species have a rather wide, continuous stylar shelf with a strong mesostyle divided into anterior and posterior segments by the transverse valley.

M. pungens has a weak paraconule and lacks a metaconule (although a small enamel fold may develop in this area). The pre- and postparaconule cristae are also weak, with the preparaconule crista extending buccally, but not joining the precingulum or the parastylar region. The postparaconule crista is often absent. In *M. malaris*, the paraconule is stronger and may be of a low shelf-like form. The preparaconule crista is stronger than in *M. pungens* but still does not join the precingulum; however, it may extend nearly to the parastylar region. The postparaconule crista is weak but may join the anterior side of the transverse valley. *M. malaris* may have a small metaconule, but it is never shelf-like. The premetaconule crista is normally absent in both species. *M. pungens* lacks a postmetaconule crista, while *M. malaris* may have a rather strong one that approaches the postcingulum.

Both species have a parastyle, while a metastyle is present only in *M. malaris*. A small stylocone may be present in *M. pungens*. Both species have weak pre- and postcingula, although *M. malaris* may have a stronger precingulum in some cases. Neither species has a hypocone on M^3 and the transverse valley is weaker on that molar in both species.

It is probable that *M. pungens* is the descendant of *M. malaris*, although Tsentas's (1981) recent demonstration that both species are present from a single locality weakens, but does not disprove this hypothesis. Previously it had been suggested (Taylor and Butler, 1980) that *M. malaris* was an index fossil for the *Tetraclaenodon/Pantolambda* Interval-Zone (To2), but this has now been proven false. However, *M. pungens* may be a good index fossil for the *Pantolambda* Zone (To3).

Mixodectes malaris Cope

Indrodon malaris Cope, 1883c, p. 318; Osborn and Earle, 1895, p. 7; Matthew, 1899, p. 29; Osborn, 1902, p. 208, figs. 33–34;
Mixodectes malaris, Matthew, 1937, p. 223, Pl.57, figs. 4–5; Szalay, 1969b, p. 215, Pl. 17, figs. 5–10, Pl. 21, figs. 4–11, Pl. 22, figs. 1–4; Taylor, 1981, p. 258; Tsentas, 1981, p. 271; Rigby, 1981, p. 63.
Mixodectes sp., Rigby, 1980, p. 63.

Holotype.—AMNH 3080, a palate preserving part of left P^3, P^4-M^3, and right C^1?, P^4-M^3, teeth all badly broken, and a broken mandible.

Age and Distribution.—*Tetraclaenodon/Pantolambda* Interval-Zone (To2) to *Pantolambda/Plesiadapis praecursor* Interval-Zone (To3), Torrejonian, middle Paleocene, Nacimiento Formation, San Juan Basin, New Mexico, and Fort Union Formation, Swain Quarry, Carbon County, Wyoming.

Diagnosis.—Differs from *Mixodectes pungens* in being smaller, by having relatively smaller upper and lower P4's, by having a more trenchant P_4 talonid, by lacking or having weak mesoconids on lower molars, by having slightly weaker transverse valleys on upper molars, by having stronger paraconules and a better developed precingulum on upper molars, and by lacking a stylocone.

Discussion.—*Mixodectes malaris* was the type species of Cope's genus *Indrodon*. Matthew (1937) synonymized *Indrodon* with *Mixodectes* maintaining a distinct species for Cope's genus. The type specimen is so badly damaged that it was difficult to recognize its true affinities with *Mixodectes*. Even today the number of good specimens of *Mixodectes* are relatively few, leading Tsentas (1981) to question the validity of *M. malaris*. Under the discussion for *M. pungens*, I have pointed out a number of differences between the two species that I feel warrant specific separation. Future collecting will provide information to support or refute this hypothesis.

Mixodectidae, *incertae sedis*
Eudaemonema Simpson, 1935

Eudaemonema Simpson, 1935, p. 231; Simpson, 1937a, p. 131; Van Valen, 1967, p. 261; McKenna, 1960b, p. 261; Szalay, 1969b, p. 224.

Type Species.—Eudaemonema cuspidata.

Included Species.—Type only.

Diagnosis.—Eudaemonema differs from *Mixodectes* and *Dracontolestes* in a number of features including: 1) the presence of a submolariform P_4 with a low shelf-like paraconid with a strong paracristid, a good metaconid subequal in height to the protoconid, and a strong three cusped talonid basin; 2) the presence of a strong mesoconid on lower molars (approached by *M. pungens*); 3) an oblique cristid that joins the postvallid of the trigonid centrally; 4) the presence of a sloping, buccally extended hypoflexid; 5) a very weak to absent entocristid and a U-shaped talonid notch; 6) presence of very strong and shelf-like paraconules and metaconules; 7) presence of a very strong hypocone, formed not on the posterior aspect of the protocone as in *Mixodectes*, but on the posterior lingual aspect of the basal cingulum and separated from the protocone by a distinct, deep, V-shaped crevice; 8) presence of a very strong preparaconule crista that joins the parastylar region, and a strong, short postparaconule crista; 9) presence of a short, strong premetaconule crista and a very strong postmetaconule crista that joins the metastylar region; 10) presence of very strong pre- and postcingula that are joined lingually and that proceed strongly buccally, dorsal to the preparaconule and postmetaconule cristae; 11) presence of a semimolariform P^4 with a small metacone and a weak paraconule; 12) and by the retention of two additional teeth (upper and lower canine and upper and lower P1).

Eudaemonema cuspidata Simpson, 1935

Eudaemonema cuspidata Simpson, 1935, p. 231; Simpson, 1937a, p. 131, figs. 25–26; Szalay, 1969b, p. 225, Pl. 25, figs. 1–9, Pl. 26, figs. 1–2.

Holotype.—USNM 9314, left mandible with roots of I_{1-2}, C_1, root of P_1, and P_2-M_3, from Gidley Quarry, Fort Union Formation, Crazy Mountain Field, Montana.

Age and Distribution. — *Pantolambda/Plesiadapis praecursor* Interval-Zone (To3), middle Paleocene of Gidley and Silberling Quarries in the Fort Union Formation of Montana, and Rock Bench Quarry, Fort Union Formation in Wyoming. Also known from the Shotgun fauna, Keefer Hill, early Tiffanian (late Paleocene), Fort Union Formation in Wyoming.

Diagnosis.—As for genus.

Discussion.—Simpson (1935) described *Eudaemonema cuspidata* and put it in Mixodectidae as we have seen, although he was unsure that it truly belonged in that family. His major reason for including it in mixodectids was that it was morphologically intermediate between *Mixodectes* and *Dracontolestes*, the two Torrejonian mixodectids and *Cynodontomys* and *Microsyops*, the two Wasatchian mixodectids (at least, according to Simpson). McKenna (1960b) pointed out that *Eudaemonema* is not intermediate between the Torrejonian and Wasatchian taxa. McKenna noted that Simpson's misidentification of a *Cynodontomys angustidens* specimen as representing P^{3-4} instead of P^4-M^1 (the correct identification) led Simpson to believe that *Cynodontomys* had a molariform upper P^4, thus making *Eudaemonema*'s semimolariform P^4 intermediate between the premolariform P^4 of *Mixodectes* and the molariform P^4 of *Cynodontomys*. McKenna (1960b) further strengthened his argument by pointing out that *Cynodontomys alfi*, a new species that he named, is older than *Cynodontomys angustidens* and has a very premolariform P^4, further refuting Simpson's hypothesis. McKenna, as it turns out, was correct in rejecting the intermediate position of *Eudaemonema*, but not because of the evidence provided by *C. alfi*. He too misidentified the P^4 of *C. alfi*, as the tooth does not belong to that taxon (see below). However, further evidence provided by *Arctodontomys wilsoni* (see Gunnell, 1985, and below) confirms McKenna's suggestion that primitive microsyopids do indeed have premolariform upper (and lower) fourth premolars. McKenna went on to remove *Eudaemonema* from mixodectids and put it in Tupaioidea, *incertae sedis*. McKenna (1966), Van Valen (1967), and Szalay (1969b) all cast considerable doubt on this assignment and the latter two authors returned *Eudaemonema* to mixodectids.

Eudaemonema cuspidata, in my view, is very different from *Mixodectes* and it is only with historical hindsight (Cope's original linking of *Mixodectes* and *Microsyops*) that it is possible to understand the persistent grouping of these two taxa together. *Eudaemonema* shares very few characters with *Mixodectes* and *Dracontolestes* that are not either primitive for the group or convergent characteristics. *Eudaemonema* shares with *Mixodectes* the following characteristics: 1) an enlarged central incisor, to varying degrees laterally compressed and a smaller lateral incisor; 2) low, shelf-like paraconids on lower molars; 3) a molar metaconid taller than (or equal in height to) the protoconid and entoconid taller than hypoconid; 4) a well developed lower molar mesoconid (only in *Mixodectes pungens*); 5) strong transverse valleys on upper molars; 6) and upper fourth premolars lacking conules or a transverse valley.

Of these characters, an enlarged I_1 is not diagnostic of mixodectids, since palaechthonids, plesiadapids, carpolestids, apatemyids, paromomyids, and some dermopterans (see Bown and Rose, 1979, and below), as well as possibly *Purgatorius* (see Kielan-Jawoworska, Bown, and Lillegraven, 1979) all have enlarged central incisors that are laterally compressed to varying degrees. Retention of a lateral incisor is primitive and not diagnostic. Low shelf-like paraconids are shared with *Purgatorius* and are probably primitive for plesiadapiforms. A metaconid taller than the protoconid and an entoconid taller than the hypoconid is shared with *Mixodectes*, but is also shared with dermopterans and cannot be used to surely place *Eudaemonema* with either group. A well developed molar mesoconid is a variable character common to a number of taxa (for example *Torrejonia*, *Plesiolestes*, dermopterans) and variable within a species, so the probability of convergence is rather high and reduces the taxonomic usefulness of this characteristic. A well developed transverse crest on upper molars resulting in dilambdodonty is not only common in *Mixodectes* and *Eudaemonema* but is also shared with dermopterans. *Craseops*, a late Eocene microsyopid, also exhibits secondarily derived dilambdodonty; see below. Finally, upper fourth premolars lacking conules and transverse valleys is also likely to be a primitive feature for plesiadapiforms.

Other features, while appearing similar between *Mixodectes* and *Eudaemonema*, are quite different when examined closely. Szalay (1969b) stressed the similarity of the upper molar conules in the taxa that he united in Mixodectidae. As was discussed above, *Mixodectes* has rather weak conules, only *M. malaris* exhibiting a fairly strong paraconule. In *Eudaemonema* the conules form strong shelf-like projections, extending lingually from the bases of the paracone and metacone. They are triangular in occlusal outline with the apex of the triangle pointing lingually, and with their bases anchored in the lingual slope of the paracone and metacone (paraconule and metaconule). The sides are formed by strong conule cristae that project above the surface of the trigon basin. The preparaconule crista and the postmetaconule crista are very strong, wrapping around the anterior aspect of the paracone and the posterior aspect of the metacone, respectively, to join the stylar shelf. The postparaconule crista and the premetaconule crista are both strong, but rather short, joining the sides of the transverse valley. These strong conules, shelf-like in morphology, and the strong conule cristae are shared with the dermopteran *Elpidophorus* and distinguish both from *Mixodectes*.

Unlike dermopterans, *Eudaemonema* has a very strong hypocone, a characteristic shared with *Mixodectes*. However, the morphology of the hypocone differs in the two genera. As we have seen, *Mixodectes* has a hypocone that forms on the posterior flank of the protocone below the postprotocrista. It is not separated from the protocone by a deep crevice but is only slightly differentiated from the posterior slope of the protocone. In *Eudaemonema*, the hypocone forms on the strong basal cingulum, wrapping around the lingual aspect of the upper molars and extending buccally. The hypocone, while large, is separated from the protocone and postprotocrista by a deep V-shaped crevice which serves to further differentiate these two cusps.

Eudaemonema also appears to exhibit some unique features that serve to indicate its aberrant position. The molar trigonids are more open than is typical of either *Mixodectes* species or any dermopteran, and there is a weak postcingulid on the lower molars that, while shared with dermopterans, is not as strongly developed as in that group. The hypoconulid on the third molar is very strongly separated from both the hypoconid and entoconid, not more strongly connected to the entoconid as in *Mixodectes*. The molar oblique cristid joins the postvallid of the trigonid centrally, although this is also the case in *Purgatorius* and may represent a primitive retention from plesiadapiform ancestry. The molar entocristid is very weak and the talonid notch is deep, lingually sloping and U-shaped, a condition unlike most other plesiadapiforms, but approached in some *Mixodectes pungens* specimens and secondarily derived in *Craseops* and some *Microsyops* species. The strong postmetaconule crista that joins the metastylar region dorsal to the postcingulum also may be unique. Some dermopterans have strong postmetaconule cristae, but they almost always join the postcingulum instead of remaining separate from it (for example in *Elpidophorus*, *Worlandia*, and *Plagiomene*). Finally, a semimolariform upper fourth premolar differentiates *Eudaemonema* from *Mixodectes* (premolariform) and dermopterans (completely molariform) and may be unique to *Eudaemonema*.

Certain other features of *Eudaemonema* suggest that it may be related to dermopterans. As was previously noted, the semimolariform P_4 is most closely approached in morphology by the P_4 in *Elpidophorus*, although in that genus, P_4 is even more molarized. The form of the P_4 paraconid is similar in both genera. In *Eudaemonema*, it is centered on the tooth, low and semicuspidate (although it may take the form of a small shelf). In *Elpidophorus* the paraconid is also centered, but differs from that of *Eudaemonema* by being truly cuspidate and extended anteriorly. In both genera, the P_4 has a very well developed metaconid that is only slightly lower than the protoconid and slightly posterior to that cusp. Both genera also have the talonid basin of P_4 well formed with two to three distinct cusps present. As was noted above, both genera share strong, shelf-like upper molar conules, as well. An unreduced dental formula is also typical of dermopterans. *Worlandia* and *Elpidophorus* share the same upper and lower dental formula of 2–1–4–3 with *Eudaemonema*, while *Plagiomene* retains an extra incisor, at least in the lower dentition, for a lower dental formula of 3–1–4–3. *Eudaemonema* differs from dermopterans by the presence of a large hypocone, the lack of skewed or angled lower molar trigonids and talonids, and the lack of well developed lower molar cingulids.

Simpson (1937) and Szalay (1969b) rejected dermopteran affinities for *Eudaemonema* (or for mixodectids in general) because (I have noted the exceptions in parentheses): 1) plagiomenids have double mesostyles (this is not the case in all plagiomenids as *Planetetherium* and *Elpidophorus* both lack this characteristic); 2) no plagiomenids have reduced numbers of anterior teeth or enlarged central incisors (the plagiomenid *Worlandia* has lost an incisor (I_3), reduced another (I_2) and has the lower central incisor enlarged); 3) the hypoconulid is not displaced towards the entoconid in plagiomenids (in both *Worlandia* and *Elpidophorus* this occurs); 4) plagiomenids have deep cheek teeth with a number of accessory cusps (*Worlandia* does not show this characteristic as strongly as some other plagiomenids; however, this may be a valid distinction between plagiomenids and *Eudaemonema*).

Eudaemonema remains an enigmatic genus. I believe that it shows more features which link it with dermopterans than with mixodectids, yet prefer to retain it in mixodectids, *incertae sedis* until more information becomes available. Szalay (1969b) felt that *Eudaemonema* was perhaps the most morphologically primitive genus of mixodectids. I cannot agree with this assessment and feel that both *Mixodectes* and *Eudaemonema* have a number of derived characters which show that they were not closely related and had diverged in different directions from other plesiadapiforms. In many ways, *Eudaemonema* is most similar to the European genus *Remiculus*, which I discuss next, and it is possible that both genera were close to the ancestry of dermopterans.

Order DERMOPTERA ? Illiger, 1811
Family Uncertain
Remiculus Russell, 1964

Remiculus Russell, 1964, p. 72; Szalay, 1969b, p. 228.

Type Species.—Remiculus deutschi.

Included Species.—Type species only.

Diagnosis.—*Remiculus* differs from *Mixodectes* by having a more molariform P_4, cuspidate lower molar paraconids, well developed anterior and posterior cingula on lower molars, a sloping, buccally extended hypoflexid, strong, shelf-like upper molar conules, with well developed conule cristae, a small, uninflated hypocone developed on a basal cingulum, and a fairly strong stylocone (variably present but weak in *Mixodectes pungens*). *Remiculus* differs from *Eudaemonema* by having a slightly less well developed P_4 talonid, cuspidate lower molar paraconids, well developed lower molar anterior and posterior cingula, lacking lower molar mesoconids (or having them very weakly developed), an oblique cristid that joins the postvallid of the trigonid buccal of center, a strong entocristid that closes the talonid lingually, a small, uninflated hypocone, and having a stylocone. *Remiculus* differs from *Elpidophorus* (the earliest recognized dermopteran) by having P_4 less molariform with a weaker shelf-like paraconid, cuspidate molar paraconids, small to weak lower molar mesoconids, upper molar cingula that join lingually, and having a stylocone.

Age and Distribution.—Late Paleocene (Thanetian) of France.

Remiculus deutschi Russell, 1964

Remiculus deutschi Russell, 1964, p. 72, Pl. 6, figs. 1–3; Szalay, 1969b, p. 229, Pl. 23, figs. 5–8.

Holotype.—CR312, left upper second molar, from Cernay-les-Reims, on the west slope of Mont de Berru, France.

Age and Distribution.—Type and all other specimens are from Cernay-les-Reims, late Thanetian (late Paleocene), France.

Diagnosis.—As for genus.

Discussion.—Russell (1964) rejected McKenna's (1960b) assignment of *Eudaemonema* to tupaioids and *Elpidophorus* to plesiadapoids (both *incertae sedis*). He noted for *Elpidophorus*, that while the buccal (ectoloph) portions of the upper molar were somewhat similar to plesiadapids, the lingual portions were completely different. He also pointed out that the upper premolars were much more molariform in *Elpidophorus* than in plesiadapids. He moved *Elpidophorus* back into Mixodectidae. As for *Eudaemonema*, Russell felt that despite dental similarities between it and living tree shrews, it was closer in morphology to its contemporary, *Mixodectes*, so he moved *Eudaemonema* back into Mixodectidae, as well. He noted that mixodectids were "primatoid" in nature, but chose to retain them in Insectivora.

Russell (1964) described the new genus *Remiculus* as a mixodectid and stated that *Elpidophorus* and *Eudaemonema* approached it in morphology most closely. Russell felt that the lower molars of *Remiculus* with their rather tall metaconids and entoconids, and their lack of buccal cingulids resembled *Eudaemonema* more closely, but he did note that *Remiculus* had lingually closed talonids (with a strong entocristid). He noted that the upper molars were intermediate between the two North American taxa, particularly in hypocone morphology. He also noted that in the form of the lower molars (especially the position of the paraconid, the lingual closure of the talonid, and the absence of a buccal cingulid), *Remiculus* approached the morphology of *Dracontolestes*.

Examining the dental evidence closely reveals some interesting comparisons. *Remiculus* shares with the *Mixodectes*/*Dracontolestes* group the following characteristics: 1) small lingual to central-lingual hypoconulids on M_{1-2} (M_3 is unknown in *Remiculus*); 2) a molar metaconid slightly taller than the protoconid; 3) a talonid closed by a rather strong entocristid; 4) a strong transverse valley on upper molars; 5) and a less well developed P_4 talonid than is typical of either *Elpidophorus* or *Eudaemonema*. *Remiculus* also shares with *Dracontolestes* a more cuspidate, anteriorly oriented lower molar paraconid. Among these characters, there are few, if any, which support a strong relationship between the European genus and North American mixodectids. A small, lingual to central-lingually positioned hypoconulid is common to all of these taxa under discussion and may be primitive for plesiadapiforms (especially on M_{1-2}; hypoconulids on M_3 tend to differ among the taxa, but none are yet known of *Remiculus*). Molar metaconids and entoconids taller than protoconids and hypoconids, respectively, are also shared by *Eudaemonema* and by *Elpidophorus* and are no indication of close affinities between *Remiculus* and *Mixodectes/Dracontolestes*. Talonids closed by rather strong entocristids and strong upper molar transverse valleys are also typical of dermopterans. A less well developed P_4 talonid with a fairly strong entoconid and a paracristid is shared with *M. pungens*, but is derived compared to *M. malaris*. Convergence cannot be ruled out in this case, particularly since the other aspects of P_4 morphology are quite different between the two genera. A more anteriorly extended, cuspidate (or less shelf-like, in the case of *Dracontolestes*) molar paraconid may represent a shared, derived characteristic between *Dracontolestes* and *Remiculus*, although lacking other evidence, convergence cannot be ruled out.

Among dental characteristics shared between *Remiculus* and *Eudaemonema* are the following: 1) a semimolariform P_4 with a low, shelf-like paraconid and a well developed metaconid; 2) sloping, shelf-like (buccally extended) hypoflexids; 3) strong, shelf-like upper molar conules; 4) strong preparaconule cristae that join the parastylar region and strong but short postparaconule cristae; 5) upper molar cingula that are joined lingually; 6) hypocones formed on posterior basal cingula and separated from the protocone and postprotocrista. Only the form of the molar hypoflexid and of the paraconule cristae appear to be primitive. The other characters are probably derived, and among them the low, shelf-like paraconid of P_4, the lingually joined upper molar cingula, and the hypocone developed on the basal cingulum, may represent shared, derived characters (although again convergence is a possibility). The other characters listed above (a well developed P_4 metaconid, a semimolariform P_4, and shelf-like upper molar conules) are shared with *Elpidophorus* and other dermopterans.

In addition to those characters, *Remiculus* also shares the following with *Elpidophorus*: 1) a slight anterior-lingual to posterior-buccal orientation of lower molar trigonids; 2) good anterior and posterior lower molar cingulids (*Remiculus* has a weak buccal cingulid *Elpidophorus* has a well developed buccal cingulid); 3) a small, uninflated hypocone on upper molars; 4) and a strong postmetaconule crista that does not join the metastylar region. The oblique orientation of the lower molar trigonids is typical of most dermopterans, as are rather well developed lower molar cingulids. The hypocone of *Remiculus* is not enlarged as is typical of *Eudaemonema* or *Mixodectes*, but is quite small as in *Elpidophorus*. However the hypocone differs from *Elpidophorus* by being formed on a basal cingulum as in *Eudaemonema*. *Elpidophorus* has a hypocone similar in form to *Mixodectes* (that is, developed on the posterior flank of the protocone below the postprotocrista) but is not very enlarged as is typical of *Mixodectes*. A strong postmetaconule crista that does not extend to the metastylar region (as it does in *Eudaemonema*) is shared between only *Remiculus* and *Elpidophorus*. In addition, *Remiculus* shows the typical closed talonid condition with the strong entocristid as in *Elpidophorus* (but also shared by *Mixodectes* to some extent).

MIXODECTID RELATIONSHIPS

In an attempt to better understand the relationships among the genera which have been included in mixodectids and the relationships between these genera and other plesiadapiform families, I have examined twenty-eight dental characteristics (see Table 8).

Taxa included in the comparisons are the mixodectids *Mixodectes* (both *M. pungens* and *M. malaris*), *Eudaemonema cuspidata*, and *Dracontolestes aphantus*, the dermopterans *Remiculus*, *Elpidophorus* (both *E. minor* and *E. elegans*), *Worlandia inusitata*, and *Plagiomene multicuspis*. An hypothetical ancestral morphotype was constructed (based on the above taxa along with *Purgatorius*, *Palaeoryctes*, and *Procerberus*).

PAUP (Phylogenetic Analysis Using Parsimony, Swofford, 1985, version 2.4) analysis was run on these 28 characters. The branch-and-bound option was employed to insure that the most parsimonious tree of all possible trees was found. Characters were weighted equally so that those characters with more states than others were not overemphasized. Figure 20 shows the cladogram derived from the analysis.

Most of the relationships proposed in the systematics section concerning these taxa are supported by this analysis. *Worlandia* and *Plagiomene* are sister taxa, with *Remiculus* and *Elpidophorus* being members of the fossil dermopteran clade, as well. *Eudaemonema* is the sister taxon to this clade, sharing a semimolariform lower fourth premolar, and a relatively strong upper molar transverse valley. However, it differs from fossil dermopterans by having a very strong hypocone, and an enlarged, compressed, lower central incisor, unlike any known for dermopterans. The characters shared between *Eudaemonema* and dermopterans may well be homoplasic (especially a semimolariform premolar), although the presence of a transverse valley on M^1 does support a relationship.

Mixodectids are more distantly related sharing a suite of features that are all likely to be homoplasies. There is a small development of a transverse valley on mixodectid

Table 8. Comparative dental characters of various plesiadapiform and dermopteran species.

Species	I	P_3	P_4	P_4 paraconid	P_4 metaconid	P_4 talonid	Molar paraconid	Molar metaconid	Molar trigonid
Elpidophorus minor	?	premolariform	molariform	cuspidate large	cuspidate low	3 cusped	shelf-like	elevated	angled
Elpidophorus elegans	I^1 enlarged tricuspate	semi molariform	molariform	cuspate large	?	2–3 cusped	shelf-like	elevated	angled
Eudaemonema cuspidata	I_1 enlarged compressed	premolariform	semi-molariform	shelf-like low	cuspidate	3 cusped	shelf-like low	elevated	not angled
Mixodectes malaris	I_1 enlarged semicompressed	premolariform	premolariform semi-enlarged	small	absent	1 central cusp	shelf-like low	weakly elevated	not angled
Mixodectes pungens	I_1 enlarged compressed	premolariform	premolariform enlarged	small to absent	absent	1–2 cusped	shelf-like	elevated	not angled
Remiculus deutschi	?	?	semi-molariform	shelf-like low	strong cuspidate	2 cusped	cuspidate	not elevated	angled
Dracontolestes aphantus	?	?	?	?	?	?	shelf-like	weakly elevated	not angled
Worlandia	I_1 enlarged bicuspate	semi-molariform	molariform	cuspidate	low cuspidate	3 cusped	cuspidate	not elevated	angled
Plagiomene	I_1 bicuspate	semi-molariform	molariform	shelf-like	cuspidate	3 cusped	cuspidate	weakly elevated	angled

Species	Molar cingulids	Molar entoconid	Molar hypoconulid	Molar mesoconid	Molar oblique cristid	Molar hypoflexid	Molar entocristid	M^1 transverse valley	Molar conules	Molar hypocone
Elpidophorus minor	strong	elevated	distinct lingual	absent	joins buccal center	sloping shelf-like	strong	?	?	?
Elpidophorus elegans	strong	elevated	weak lingual	developed	joins buccal center	sloping shelf-like	strong	very strong	strong shelf-like	weak not separate
Eudaemonema cuspidata	weak	weakly developed	small lingual	strong	joins buccal center	sloping shelf-like	weak	strong	strong shelf-like	very strong separate
Mixodectes malaris	absent	elevated	small lingual	weak	joins buccal	steep not shelf-like	developed	developed	semi-shelf-like weak	strong not separate
Mixodectes pungens	weak	elevated	small lingual	strong	joins buccal	steep not shelf-like	weak	developed	weak not shelf-like	strong not separate
Remiculus deutschi	strong	weakly developed	small lingual	weak	joins buccal center	sloping shelf-like	developed	strong	strong shelf-like	small separate
Dracontolestes aphantus	absent	not elevated	small centered	weak	joins buccal	steep not shelf-like	strong	?	?	?
Worlandia	strong	elevated	small semi-lingual	absent	joins buccal	steep not shelf-like	very strong	very strong	very strong shelf-like	absent
Plagiomene	strong	elevated	small central	weak	joins buccal	steep not shelf-like	very strong	very strong	very strong shelf-like	absent

Table 8. (continued)

Species	Paraconule crista	Metaconule crista	Molar cingula	Stylar shelf	Stylocone	p^4	p^4 conules	p^4 transverse valley	Dental formula
Elpidophorus minor	?	?	?	?	?	?	?	?	?
Elpidophorus elegans	*pre-strong post-strong*	*pre-strong post-developed*	*strong*	*developed*	*absent*	*molariform*	*strong shelf-like*	*weak*	*2?-1-4-3*
Eudaemonema cuspidata	pre-strong post-strong	pre-strong post-very strong	very strong	developed	absent	semi-molariform	weak	absent	2?–1–4–3
Mixodectes malaris	pre-weak post-weak	pre-weak post-weak	developed	developed	absent	premolariform semi-enlarged	absent	absent	2–0–3–3
Mixodectes pungens	pre-weak post-weak	absent	weak	strong	weak to absent	pre-molariform enlarged	absent	absent	2–0–3–3
Remiculus deutschi	pre-strong post-strong	pre-strong post-strong	weak	strong	present	?	?	?	?
Dracontolestes aphantus	?	?	?	?	?	?	?	?	?
Worlandia	pre-strong post-weak	pre-weak post-strong	strong	developed	present	molariform enlarged	strong shelf-like	developed	2–1–4–3
Plagiomene	pre-weak post-weak	pre-weak post-weak	strong	strong	strong	molariform enlarged	strong shelf-like	strong	3–1–4–3

upper molars, but nothing like that seen in dermopterans or *Eudaemonema*.

To summarize, *Dracontolestes* cannot be assessed adequately, but based on its overall similarity, there is no reason to expect that future material will alter the view that it is most closely related to *Mixodectes* and should therefore remain as a mixodectid. The other members of mixodectids, *Mixodectes malaris* and *Mixodectes pungens* are clearly closely related. *Elpidophorus elegans* and *Elpidophorus minor* are very closely related and are more closely related to *Worlandia* than to any other genus examined, while *Worlandia* and *Plagiomene* are quite closely related and share significant similarities with *Elpidophorus* and *Remiculus*. *Eudaemonema* may be more closely related to dermopterans than to mixodectids or microsyopids.

Suggestive evidence concerning the affinities of *Remiculus* also comes from the geographic distribution of this taxon. Plagiomenid dermopterans are exclusively part of the northern community fauna (see Chapter III). All of the known genera occur north of approximately 40 degrees north latitude in Sloan's (1969) northern faunal community. *Elpidophorus* (the Torrejonian and Tiffanian taxon) is known from localities in central Wyoming, northern Wyoming, south-central Montana, and south-central Alberta. *Planetetherium* (Clarkforkian taxon) is known only from northern Wyoming and southern Montana (Rose and Simons, 1977). *Worlandia* (Clarkforkian taxon) is known only from northern Wyoming and southern Montana (Bown and Rose, 1979). *Thylacaelurus* (Uintan, late Eocene taxon) is only known from British Columbia and north-central Wyoming (Russell, 1954; Szalay, 1969b; Setoguchi, 1973). *Plagiomene* (Clarkforkian and Wasatchian taxon) was, until recently only known from northern Wyoming (Rose, 1973), but it has now also been found in the Eureka Sound Formation on Ellesmere Island in the eastern Canadian Arctic (West and Dawson, 1977). The European genus *Placentidens* (Sparnacian and Cuisan taxon) is a problematic dermopteran from France and England (Russell, et al., 1982).

Remiculus is known exclusively from this northern faunal community, from the Thanetian, late Paleocene Cernay-les-Reims locality in France (Russell, etal., 1982).

Mixodectes and *Dracontolestes* are known exclusively from Sloan's southern terrestrial community. *Dracontolestes* (early Torrejonian, "Dragonian" taxon) is only known from central Utah, while *Mixodectes* is predominately known from north-western New Mexico. *Mixodectes malaris* has recently been recognized in southern-most Wyoming at the Torrejonian locality of Swain Quarry (Rigby, 1980) and from northern Colorado, Togwotee Pass area, Love Quarry (*Mixodectes* sp., McKenna, 1980), both of which are near the geographic "boundary" between Sloan's northern and southern terrestrial communities.

The presence of *Remiculus* in the northern terrestrial community and the exclusion of *Mixodectes* and *Dracontolestes* from that community makes a dermopteran relationship for *Remiculus* slightly more plausible. The presence of plagiomenid dermopterans in high latitude locali-

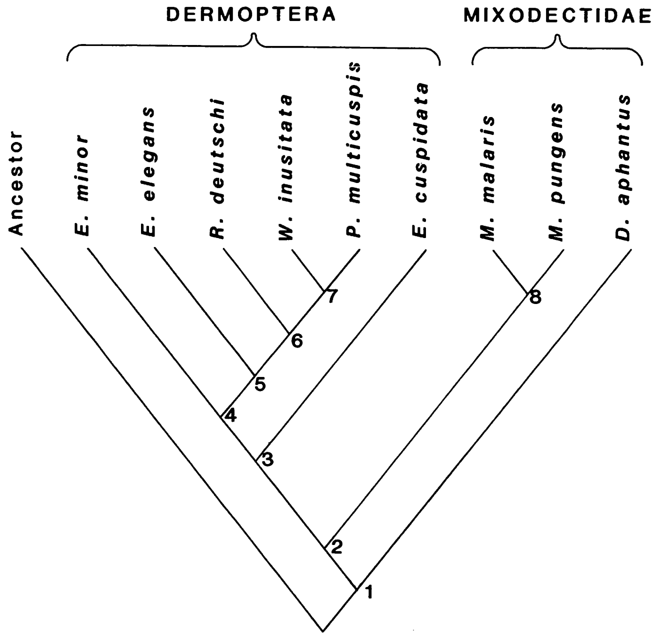

Figure 20. Cladogram showing relationships among nine taxa of mixodectids and fossil dermopterans. Cladogram is based on 17 dental characteristics. Shared, derived characters representative of each node are as follows: Node 1 - molar mesoconid weak, molar metaconid weakly elevated, molar entocristid strong, M^1 transverse valley present; Node 2 -molar entoconid elevated, molar hypoconulid small and lingually placed; Node 3 - P_4 molariform, molar metaconid elevated, molar cingulids weak, molar mesoconids strong, molar entocristid weak, pre- and postmetaconule cristae strong, P^4 semimolariform; Node 4 - P_4 paraconid and metaconid cuspidate, P_4 talonid 3 cusped, molar hypoflexid forming sloping shelf, M^1 transverse valley strong, molar conules strong and shelf-like, hypocone strong and not formed on postprotocingulum, pre- and postparaconule cristae strong, molar cingula strong, P^4 conules weak, lower dental formula of 2–1–4–3; Node 5 - I_1 bicuspate, molar trigonid angled, molar cingulids strong, molar mesoconid weak, molar entocristids strong, P^4 conules strong and shelf-like, P^4 transverse valley weak; Node 6 - P_3 semimolariform; Node 7 -P_4 paraconid shelf-like, molar paraconid cuspidate, molar metaconid not elevated, hypocone small and not formed on postprotocingulum, stylar shelf strong, stylocone present, P^4 molariform, P^4 transverse valley strong; Node 8 -hypoconulid small and centrally placed, molar hypoflexid steep, molar entocristid very strong, M^1 transverse valley very strong, hypocone absent. See text for further discussion.

ties on Ellesmere Island indicates that if a high arctic connection between Europe and North America existed during the later Paleocene, plagiomenids would probably not have been restricted from crossing this land bridge. The possibility of dermopterans existing in Europe is therefore enhanced and makes it more plausible that *Remiculus* and *Placentidens* may be dermopterans. *Eudaemonea* is also known only from the northern terrestrial community. This may support a closer relationship with dermopterans than with mixodectids.

The lack of any *Eudaemonema* or *Elpidophorus* specimens from the southern terrestrial community, along with the lack of any other recognized dermopterans from that community suggests that dermopterans may have been ecologically or historically restricted to more northern habitats. The restriction of *Eudaemonema* and *Elpidophorus* to northern habitats suggests that they may have been restricted by barriers similar to those that may have restricted dermopterans.

MICROSYOPID-MIXODECTID RELATIONSHIPS

Having demonstrated in the above sections that mixodectids should be restricted to the genera *Mixodectes* and *Dracontolestes*, I shall now turn to the possible relationships between these two taxa and Eocene microsyopids. *Arctodontomys* shares no derived characters with *Elpidophorus* or *Eudaemonema* and shares only one each with *Plagiomene* and *Worlandia* (steeply angled, not buccally extended hypoflexids) and *Remiculus* (buccal joining of the oblique cristid to the postvallid), which are almost surely convergent in nature.

Mixodectes and *Arctodontomys*, however, share a number of characters including the following: 1) a premolariform P_3; 2) a premolariform P_4 with no metaconid and a weak talonid basin; 3) lingually placed hypoconulids; 4) an oblique cristid that joins the postvallid of the trigonid buccally; 5) a steeply angled, not buccally extended hypoflexid on lower molars; 6) relatively strong entocristids forming a V-shaped talonid notch; 7) hypocone formed on the posterior flank of the protocone below the postprotocrista; 8) a premolariform P^4.

Examining the distribution of these characters more closely reveals that most are not reflective of a close relationship. A premolariform P_3 is probably primitive for plesiadapiforms. A buccal joining of the oblique cristid to the postvallid is also characteristic of most dermopterans and does not represent a special similarity between *Mixodectes* and *Arctodontomys*. Steeply angled, not buccally extended hypoflexids also are typical of *Worlandia* and *Plagiomene* and are likely to represent convergent adaptations. A relatively strong entocristid forming a V-shaped talonid notch may represent a shared, derived condition, but also may be convergent, as *M. pungens* often differs in this characteristic, as do some *Microsyops* species. The morphology is also slightly different as *Mixodectes* has a more steeply angled entocristid due to a more elevated entoconid and is slightly more open at the apex of the angle formed by the entocristid and postvallid even in *M. malaris*, which, unlike *M. pungens* never develops a wide U-shaped talonid notch. While both genera have a hypocone developed on the posterior flank of the protocone, in *Mixodectes* this cusp is very inflated and enlarged, while in *Arctodontomys* the hypocone is little more than a small fold of enamel (sometimes slightly larger). In *Arctodontomys*, the hypocone is also often connected to a posterior basal cingulum.

It is in the morphology of upper and lower P4 where *Mixodectes* and *Arctodontomys* seem most similar. The lower fourth premolar in both genera is premolariform with a tall protoconid cusp and a relatively simple talonid. The two species of *Mixodectes* seem to combine characteristics similar to those of *Arctodontomys*. In *Arctodontomys simplicidens*, P_4 is somewhat enlarged and has no trace of either a paraconid or a metaconid. The talonid consists of an elevated central cusp with both buccal and lingual sides sloping steeply away from this central cusp. This morphology is most closely mirrored in *M. malaris*, except that this species has a fairly strong paracristid running down the anterior flank of the protoconid and often has a small enamel fold developed at the termination of the paracristid that could be interpreted as a small paraconid. In addition, *M. malaris* has a central talonid cusp much less elevated than is the case in *Arctodontomys simplicidens*, resulting in less steeply angled buccal and lingual aspects. *M. pungens* is more distinct from *Arctodontomys* by having P_4 greatly enlarged, by often having a distinct paraconid cuspule, and by having a very low, flat talonid.

Upper P4 is more distinctive in the two genera even though it is premolariform in both. *Mixodectes* has a relatively more elevated protocone than *Arctodontomys*, while *Arctodontomys* may develop a tiny metacone (this cusp may be developed in *A. wilsoni*; P^4 remains unknown in *A. simplicidens*).

A plausible ancestor-descendant progression could be hypothesized based on P_4 morphology from *Purgatorius* (simple trigonid with distinct paraconid and simple talonid) to *Mixodectes malaris* (simple trigonid with reduced paraconid and simple talonid) to *Arctodontomys simplicidens* (simple trigonid with no paraconid and simple talonid), with *Mixodectes pungens* being viewed as a derived side branch. Of course, P_4 morphology is not the only characteristic of importance and in a number of other characters, *Arctodontomys* and *Mixodectes* differ considerably. The dental formulae differ in the two genera. *Mixodectes* has upper and lower dental formulae of 2–0–3–3, while in *Arctodontomys* the lower dental formula is 1–0–3–3. Thus *Arctodontomys* has lost its lateral incisor, which is no barrier for relationship. However, the upper dentition may question any close relationship between *Mixodectes* and *Arctodontomys*. The upper dental formula of *Arctodontomys* remains incompletely known, but its very close Eocene relative *Microsyops* has an upper dental formula of 2?-1–3–3. If *Arctodontomys* has the same upper dental formula as *Microsyops* (which seems likely as it does share the same lower dental formula), then it has retained an additional tooth in its upper dentition (regardless of the interpretation of the homologies), making it unlikely for *Mixodectes* itself to have been ancestral to *Arctodontomys*. It is possible that better specimens of *Mixodectes* will change our interpretation of its dental formula or that more complete specimens of *Dracontolestes* may show that it retains an additional upper tooth as does *Microsyops*, making the derivation of microsyopids from mixodectids more plausible (or that *Arctodontomys* does not retain the same number of upper teeth as *Microsyops*, indicating a more distant relationship between these two genera than now appears likely). However, dental evidence now available does not support a mixodectid origin for microsyopids. Both genera have enlarged central incisors (lowers) with laterally compressed roots (more strongly compressed in *Arctodontomys*), but *Arctodontomys* has a lanceolate, curving crown which appears to be lacking in *Mixodectes*. In *Arctodontomys*, P_2 is more robust than P_3 which is rather small and single-rooted (these characteristics apply to *A. simplicidens*. However, in *A. wilsoni*, P_2 and P_3 are similar in size and P_3 may be double-rooted; see below and Gunnell, 1985). *Mixodectes* has a less reduced P_3 which is double-rooted. Molar paraconids are low and shelf-like in *Mixodectes*, cuspidate (at least, on M_1, less so on $M_{2\text{-}3}$), more lingually extended and higher on the anterior aspect of the trigonid in *Arctodontomys*. Lingual cusps on lower molars of *Mixodectes* tend to be equal or slightly taller than the buccal cusps, while the reverse is generally true in *Arctodontomys*. The hypoconulid is lingually placed in both genera, but on M_3, *Arctodontomys* has a smaller hypoconulid, less distinctly separated from the entoconid than in *Mixodectes*. Mesoconids are variably developed in both genera.

It is in the upper molars where the two genera are clearly differentiated. *Mixodectes* has the distinct transverse valley typical of dermopterans and *Eudaemonema*. *Arctodontomys* lacks this dilambdodonty completely. In addition, as a result of this dilambdodont morphology, *Mixodectes* has a very strong, partially bisected mesostyle and a fairly well developed stylar shelf. *Arctodontomys* lacks a mesostyle completely and has a very small to absent stylar region. In *Mixodectes* upper molar conules are weak to absent, and when present (as in the paraconule of *M. malaris*) tend to be rather shelf-like. In *Arctodontomys*, both the paraconule and metaconule are rather strongly developed and cuspidate, not shelf-like. As a result of these strong conules, *Arctodontomys* has rather strong preparaconule cristae and somewhat weaker postmetaconule cristae, while the postparaconule cristae and the premetaconule cristae tend to be absent. In *Mixodectes* conule cristae, if present at all are very weak. As already noted, both genera have hypocones of similar morphology, however *Mixodectes* has a much larger and more inflated hypocone. Finally, both genera have premolariform forth upper premolars, but they differ somewhat in morphology as noted above.

Mixodectids remain difficult to evaluate systematically or functionally. This is probably a direct result of the rather small numbers of specimens and their fragmentary nature. I have difficulty in placing them in insectivores for lack of a better place, because they have surely evolved beyond a typical dental insectivore, convergent on euprimates (primates of modern aspect) in a number of ways. It is still possible that they were ancestral to microsyopids, at least in a broad sense, but appear to be too derived to hold this position. Mixodectids seem to fit more comfortably in a broad group along with plesiadapoids, microsyopoids, apatemyoids, and dermopterans which have progressed beyond "typical" insectivores, but not to the level of "typical" euprimates (adapids and omomyids). *Mixodectes* and *Dracontolestes* should be viewed as members of this broad radiation, perhaps convergent on dermopterans, but restricted to a more southern terrestrial community, while "true" dermopterans remained in northern environments.

MICROSYOPID-PALAECHTHONID RELATIONSHIPS

Van Valen (1969) included both Paromomyidae (including both Palaechthonidae and Paromomyidae of this report, see Chapter III) and Microsyopidae in the superfamily Microsyopoidea (along with plesiadapids, carpolestids, and picrodontids), implying a common origin for these families. Bown and Gingerich (1973) compared the dentitions of *Plesiolestes problematicus* (here considered a plesiolestine palaechthonid) and *Cynodontomys* (=*Microsyops*) *latidens* (a microsyopine microsyopid) and concluded that the Eocene genus *Cynodontomys* was a descendant of *Plesiolestes* or the closely related *Palaechthon*, thus expanding the number of Eocene survivors of archaic plesiadapiforms to three (the others recognized at that time were the European Eocene genus *Platychoerops*, a descendant of *Plesiadapis*, and *Phenacolemur*, a descendant of *Paromomys*). Szalay (1975, 1976, 1977) and Szalay and Delson (1979) rejected the hypothesis of Bown and Gingerich (1973), basing their argument primarily on the basicranial evidence available for *Microsyops* (*Cynodontomys*).

Bown and Gingerich (1973) noted the following dental similarities between *Plesiolestes problematicus* and *Cynodontomys* (=*Microsyops*) *latidens*: 1) both species have enlarged, procumbent lower incisors that are similar in morphological detail; 2) both species have a tall, double-rooted P_3 with a prominent protoconid, a weak paraconid, and no metaconid 3) both species have a molariform P_4 with a distinct protoconid, paraconid, and metaconid, and a basined, two-cusped talonid; 4) both species have similar lower molar morphology, with a distinct, medially located paraconid on M_1, and more shelf-like paraconids on M_{2-3}, a deep trigonid valley separating the protoconid and metaconid on all lower molars, a distinct mesoconid developed on the oblique cristid, and by having a distinct hypoconulid that is appressed to the entoconid; 5) both species have similar upper molar cusps, conules and shearing crests. They noted that the two species differed by the broader talonid basin of P_4 in *Cynodontomys*, and the more distinct metaconid and weaker hypoconid of P_4 in that species. In addition, *Plesiolestes* has an expanded anterior-buccal cingulid on its lower molars, a twinned or double-lobed hypoconulid on M_3, and has the hypoconulid and entoconid joined by a crest. In the upper molars, the principle difference is the presence of a postprotocingulum in *Plesiolestes*.

Szalay (1969b) noted the possibility that microsyopids may have been primates (here plesiadapiforms) because of the dental similarities between them and Paleocene palaechthonids. However, Szalay (1975, 1976, 1977) rejected Bown and Gingerich's assessment of the affinities between *Plesiolestes* and *Microsyops* for the following reasons: 1) he felt that Bown and Gingerich ignored the basicranial evidence available for *Microsyops*; 2) he felt that this evidence linked *Microsyops* more closely with leptictid insectivores, in particular *Leptictis* (=*Ictops*); 3) Szalay noted that Bown and Gingerich compared *Plesiolestes* to *Cynodontomys* (=*Microsyops*) *latidens*, instead of to the earlier and less derived species *Cynodontomys wilsoni* and *Cynodontomys alfi*. Szalay (1975) stated that the more primitive earlier species showed that the fourth premolar (upper and lower) in both *Cynodontomys wilsoni* (now *Arctodontomys*) and *Cynodontomys alfi* (synonymous with *Microsyops angustidens*) is premolariform, not molariform as in the later species of *Microsyops*, thus demonstrating that the molariform fourth premolar shared by *Plesiolestes problematicus* and *Cynodontomys* (=*Microsyops*) *latidens* was the result of convergence and refuted Bown and Gingerich's position.

Szalay and Delson (1979) further examined the similarities between *Cynodontomys latidens* and *Plesiolestes problematicus*. They noted that although both species share a molariform P_4, the trigonid differs morphologically in the two, with *Cynodontomys* having large, conical cusps, while *Plesiolestes* has cusps that are small, with the protoconid still dominating the trigonid. They also note that the twinned hypoconulid-entoconid typical of microsyopids is absent in *Plesiolestes* and that the hypocone construction is quite different in the two species.

Bown and Rose (1976), Gingerich (1976), and Bown (1979) have all responded to the criticisms put forth by Szalay (1975, 1976) and Szalay and Delson (1979). Bown and Rose (1976) pointed out that in *Microsyops wilsoni*, the upper P4 is not premolariform as Szalay (1969b) described, but normally possesses a metacone of varying size. They also argue that the mutability of the metaconid of P_4

in *Plesiolestes* and *Palaechthon* does not preclude either of these taxa from possible ancestry for Eocene microsyopids.

Bown (1979) argues that Szalay's reliance on basicranial features over dental features to reject a relationship between Paleocene palaechthonids and Eocene microsyopids is unconvincing, because none of the relevant Paleocene taxa preserve this region of the skull. Bown and Rose (1976), Gingerich (1976), Bown (1979), and Rose and Bown (1982) continue to group these Paleocene and Eocene taxa in a single family, Microsyopidae.

I have re-examined the dental evidence relating to the question of relationships between Paleocene palaechthonids (in the sense of this report) and Eocene microsyopids. The basicranial features of Eocene microsyopids are discussed in detail in a later section of this chapter. Included in the dental comparisons are the following taxa: *Arctodontomys, Microsyops, Plesiolestes, Torrejonia, Pronothodectes, Plesiadapis, Palaechthon, Paromomys, Premnoides, Navajovius*, and *Palenochtha* (see Table 9). *Purgatorius unio* was used to construct an hypothetical ancestral morphotype.

PAUP (Swofford, 1985) analysis was run on 19 tooth characters for these eleven plesiadapiform genera. Branch-and-bound was used to obtain the most parsimonious tree, and each character was weighted equally to avoid overemphasis of characters with multiple states. Figure 21 shows the cladogram derived from the strict consensus tree for this analysis.

Microsyopoidea and Plesiadapoidea share sister-taxon status. Within microsyopoids, Microsyopidae and Palaechthonidae are sister taxa. *Plesiolestes* and *Torrejonia* (plesiolestines) and *Palaechthon* and *Palenochtha* (palaechthonines) share sister taxa status with each other. *Microsyops* and *Arctodontomys* are sisters with *Navajovius* being the sister of this clade. Within plesiadapoids, *Pronothodectes* and *Plesiadapis* are sister taxa. Interestingly, *Premnoides* is grouped as the sister taxon of *Paromomys* by this analysis.

Examining the characters that unite *Premnoides* and *Paromomys* at node 9 (weak molar paraconid and compressed molar trigonids), it is clear that these could easily be homoplasic. Node 5 characters that unite paromomyids and plesiadapids (*Pronothodectes* and *Plesiadapis*) are all based on the upper dentition (small molar conules, strong molar cingula, tricuspate central incisors, and weak molar paracrista). *Premnoides* is not yet known from upper dentitions so these characters have no bearing on its relationships.

Premnoides shares none of the more typical paromomyid characteristics such as a very compressed, anteriorly inclined molar trigonid, a double rooted P_2 (in *Paromomys*), no mesoconid, and buccolingually inflated talonid basins. Semicompressed molar trigonids and weak paraconids are also typical of many palaechthonids (such as *Palaechthon* and *Plesiolestes*). I believe that the affinities of *Premnoides* lie more closely with palaechthonids than with plesiadapoids. Further tests of this hypothesis will come from additional fossil material. This cladogram supports most of the other hypotheses put forward concerning the other taxa in this analysis.

Examining the characters closely reveals some interesting relationships. First, *Arctodontomys* has a single, enlarged, fully lanceolate (see Chapter VII) first lower incisor. This is certainly derived beyond the condition in *Purgatorius*, and appears more derived than in any palaechthonid. Only *Plesiolestes* preserves a complete lower, central incisor among palaechthonids. It is similar in morphology to that of *Arctodontomys*, but is not as broad at its crown base, lacking the distinctive dorsal bulge typical of microsyopids (for a further discussion of the differences in incisor morphology between palaechthonids and microsyopids see Chapter VII).

The lower third premolar is primitively premolariform and double rooted in all of the Paleocene genera. In *Arctodontomys*, P_3 is also premolariform but is somewhat reduced in size. It is single rooted (in *Arctodontomys simplicidens*) or single or double rooted (in *A. wilsoni*), with double roots being secondarily derived. *Arctodontomys* also differs from the Paleocene taxa by having P_2 larger than P_3 (strikingly so in *A. simplicidens*, less so in *A. wilsoni*, where P_3 is slightly larger).

The lower fourth premolar is similar in *Arctodontomys* and certain of the Paleocene taxa, but again there are certain differences, as well. It is premolariform in *Arctodontomys, Torrejonia*, and *Paromomys*, while it is much more molariform in *Palaechthon*, and even more so in *Plesiolestes*. *Arctodontomys* lacks a paraconid or metaconid on P_4 and has a rather weak talonid basin (a central cusp in *A. simplicidens* and slightly broader in *A. wilsoni*). Both species of *Torrejonia* lack a paraconid (sometimes a weak enamel fold is developed as in *T. wilsoni*) and a metaconid, but have a slightly better developed and extended talonid basin than *Arctodontomys*. *Paromomys maturus* is similar in these features, although the talonid is often weaker and more like *Arctodontomys*. *Palaechthon* has a small to weak P_4 paraconid and metaconid and a relatively weak two-cusped talonid, while *Plesiolestes* has a small, cuspidate paraconid, a small to very distinct metaconid, and a rather strongly developed, two-cusped talonid. The absence of a paraconid is derived compared to *Purgatorius*, while the absence of a metaconid is a primitive feature, as is a weak talonid basin with a centrally located cusp whose flanks slope steeply away both buccally and lingually. In this regard *Arctodontomys* is derived only in the absence of a P_4 paraconid, remaining primitive in its lack of a metaconid and in possessing a relatively simple talonid. *Torrejonia* also is derived in the loss of a paraconid, but is further derived by the presence of a stronger, two-cusped talonid. *Plesiolestes* and *Palaechthon* are derived by possessing a metaconid and a stronger talonid basin, but remain primi-

Table 9. Comparative dental characteristics of various plesiadapiform taxa

Genus	Lower dental formula	C_1	P_2	P_3	P_4 paraconid	P_4 metaconid	P_4 talonid	I_1	P^4 metacone	P^4 parastyle
Plesiolestes	2–1–3–3	larger than P_2	single rooted	premolariform	weak	present	2 cusped strong	projecting sub-lanceolate	distinct separate	distinct not separate
Palaechthon	2–1–3–3	smaller than P_2	single rooted	premolariform	weak	absent	2 cusped	?	small not separate	distinct separate
Premnoides	1–1–3–3	equal to P_2	single rooted	premolariform	absent	absent	1 cusped	?	?	?
Palenochtha	1–1–3–3	equal to P_2	single rooted	premolariform	weak	absent	2 cusped	procumbent sub-lanceolate	distinct separate	distinct separate
Paromomys	2–1–3–3	larger than P_2	double rooted	premolariform	absent	absent	2 cusped	?	absent	weak
Torrejonia	?	?	?	premolariform	weak	absent	2 cusped strong	?	?	?
Navajovius	1–1–3–3	equal to P_2	single rooted	premolariform	absent	weak	2 cusped	procumbent semi-lanceolate	absent	distinct separate
Arctodontomys	1–0–3–3	absent	single rooted	premolariform	absent	absent	1 cusped	procumbent lanceolate	small not separate	weak
Microsyops	1–0–3–3	absent	single rooted	premolariform	absent	present	2 cusped	procumbent lanceolate	small not separate	weak
Pronothodectes	2–1–3–3	equal to P_2	single rooted	premolariform	absent	absent	1 cusped	projecting caniniform	small not separate	weak
Plesiadapis	1–0–(2–3)–3	absent	single rooted or absent	premolariform	absent	absent	1 cusped	projecting caniniform	small not separate	weak

Genus	Molar mesoconid	Molar paraconid	Molar trigonid	Molar hypoconulid	Molar conules	Molar hypocone	Molar cingula	Molar paracrista	Molar metacrista
Plesiolestes	developed	small cuspate	semi-compressed	developed	developed	small PPC	weak	developed	developed
Palaechthon	absent	small cuspate	compressed	developed	developed	small PPC	developed	developed	developed
Premnoides	developed	weak	compressed	developed	?	?	?	?	?
Palenochtha	absent	distinct	open	developed	developed	small PPC	developed	developed	distinct
Paromomys	absent	weak	strongly compressed	absent	absent	large PPC	strong	weak	weak
Torrejonia	weak	small cuspate	semi-compressed	developed	developed	small PPC	weak	developed	distinct

Table 9. (continued)

Genus	Molar mesoconid	Molar paraconid	Molar trigonid	Molar hypoconulid	Molar conules	Molar hypocone	Molar cingula	Molar paracrista	Molar metacrista
Navajovius	weak	distinct	open	developed	weak	small not PPC	weak	developed	weak
Arctodontomys	weak	small cuspate	semi-compressed	small twinned	developed	small not PPC	weak	developed	developed
Microsyops	developed	small cuspate	semi-compressed	small twinned	developed	small not PPC	weak	developed	weak
Pronothodectes	weak	small cuspate	semi-compressed	developed M_3 expanded	weak	small PPC	developed	weak	weak
Plesiadapis	weak	small cuspate	semi-compressed	developed M_3 expanded	weak	small PPC	developed	weak	weak

tive by retaining the P_4 paraconid. It is possible that *Purgatorius* represents a derived condition by possessing a P_4 paraconid, although other Cretaceous taxa such as *Procerberus* and *Protungulatum* also possess P_4 paraconids (and metaconids as well), but of a differing morphology from that of *Purgatorius* (see Chapter III). The plesiolestine *Torrejonia* has a more simplified P_4 than does *Plesiolestes* and it is possible that the absence of a metaconid is secondarily derived in *Torrejonia* and represents an overall trend towards P_4 simplification in the plesiolestine lineage. If this is the case, *Arctodontomys simplicidens* could be viewed as a continuation of this trend, with later *Arctodontomys* and *Microsyops* species secondarily molarizing their lower fourth premolars.

Lower molar morphology makes up the most similar set of characters shared by all of these taxa. *Arctodontomys* and all of the Paleocene taxa differ from *Purgatorius* by having a cuspidate, not shelf-like paraconid on lower molars. In *Palaechthon* and *Plesiolestes*, molar paraconids are sharp and distinct on M_1, and lower and more lingual (but still distinct) on M_{2-3}. In *Arctodontomys* and *Torrejonia*, molar paraconids are more bulbous and slightly lower on M_1 than in *Palaechthon* or *Plesiolestes*, and are lingual, low, and very small on M_{2-3}. In *Paromomys*, the paraconid is present and cuspidate on M_1, but is virtually absent on M_{2-3}. *Arctodontomys* and *Torrejonia* share more bulbous and rounded metaconids, protoconids, and entoconids, while in *Plesiolestes* and *Palaechthon* these cusps tend to be more gracile and sharper. The lower molar trigonids become progressively more anterior-posteriorly compressed, from a moderate compression in *Plesiolestes* and *Palaechthon*, to more compressed in *Torrejonia* and *Arctodontomys*, to strikingly compressed in *Paromomys* (particularly M_{2-3}).

The development and positioning of the molar hypoconulids in these taxa has been the center of much discussion. In *Arctodontomys*, the hypoconulid is lingually positioned and separated from the entoconid by a distinct, but relatively narrow notch (the distinctive "twinned" hypoconulid-entoconid characteristic of Eocene microsyopids). Bown and Gingerich (1973) noted that *Plesiolestes* had a hypoconulid that was positioned somewhat lingually, but that it differed from the condition in microsyopids by being connected to the entoconid by a crest instead of being separated by a notch (which they suggest is functionally related to the development of a hypocone and the loss of the primitive postprotocingulum typical of *Plesiolestes*). Later, Bown and Rose (1976) agreed with Bown and Gingerich (1973) and also stated that *Palaechthon* and to a lesser extent, *Navajovius*, also agreed with *Plesiolestes* in hypoconulid morphology. Szalay and Delson (1979) stated that the "twinned" hypoconulid-entoconid is not present in *Plesiolestes* and that mixodectids and tupaiids share a similar hypoconulid morphology with microsyopids.

I have recently examined all of the relevant taxa and find that none of the taxa mentioned above have hypoconulids that appear homologous to those of microsyopids, although some taxa approach the condition exhibited by the Eocene group.

Morphologically, the mixodectid *Mixodectes* and the possible mixodectid *Eudaemonema* approach the condition seen in *Arctodontomys* the closest (see Chapter VII for a discussion of dental function in mixodectids, microsyopids, and palaechthonids). Both genera share with *Arctodontomys* a hypoconulid that is lingually positioned and separated from the entoconid by a notch. However, the notch is deeper and more steeply sided in *Arctodontomys*, while in *Mixodectes* and *Eudaemonema*, the notch is shallower and is often traversed by a weak crest. The occlusal relationship with the upper teeth is also distinct between the mixodectids and *Arctodontomys*. In *Arctodontomys*, the hypocone occludes in the notch, separating the hypoconulid and entoconid, its buccal and lingual flanks shearing across the walls of the entoconid-hypoconulid notch. In *Mixodectes* and *Eudaemonema*, the hypocone occludes behind this notch and during mastication wears against the

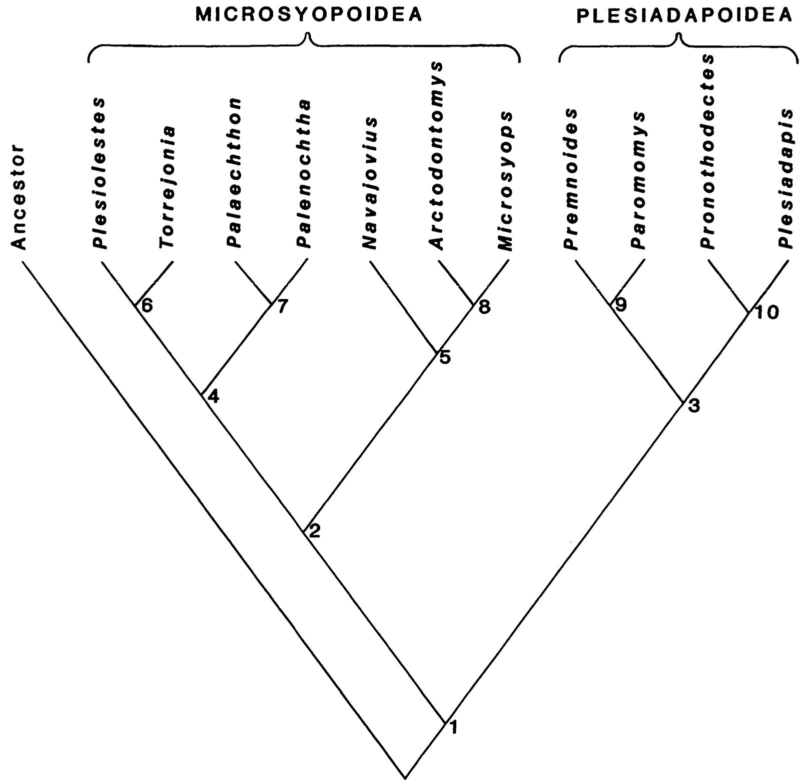

Figure 21. Cladogram showing relationships of eleven plesiadapiform taxa based on 19 dental characteristics. The ancestral condition is based on *Purgatorius unio*. Cladogram is derived from consensus tree output of PAUP analysis (Swofford, 1985; see text also). Shared, derived characters representative of each node are as follows: Node 1 - I_1 procumbent, enlarged; C_1 and P_2 equal in size, molar mesoconid weak, hypocone small and formed on postprotocingulum, molar cingula weak, P^4 parastyle weak, molar trigonids semicompressed, hypoconulids small; Node 2 -P_4 talonid 2–3 cusped, I_1 semilanceolate, P^4 parastyle distinct but not separate; Node 3 - P_4 paraconid weak, P^4 metacone distinct and separate, upper molar metacrista developed; Node 4 - lower dental formula of 1–1–3–3, P_4 metaconid weak, hypocone small and not formed on postprotocingulum; Node 5 - molar conules small, molar cingula strong, molar paracrista weak; Node 6 - C_1 larger than P_2, P_4 talonid 2 cusped and strong; Node 7 - P^4 parastyle distinct and separate, molar mesoconid absent, molar cingula present; Node 8 - lower dental formula 1–0–3–3, C_1 absent, I_1 lanceolate, P^4 parastyle weak, molar hypoconulid small and twinned; Node 9 - molar paraconid weak, molar trigonid compressed; Node 10 - M_3 hypoconulid expanded and shelf-like, I^1 tricuspate. See text for further discussion.

shelf-like paraconid of the tooth posterior to it and across the posterior and buccal surfaces of the hypoconulid, down the postcingulid. Given the functional differences between these two systems, it is likely that twinning of the hypoconulid and entoconid shared between these two groups is convergent.

A similar case can be made for twinning of the hypoconulid and entoconid in tupaiids. Normally in tupaiids, the hypoconulid is positioned very lingually, posterior to the entoconid (in some cases it is slightly more buccal than the entoconid) and separated from it by a shallow notch. In *Ptilocercus*, the hypoconulid is positioned more buccally than in the other tupaiid species (see Butler, 1980). In tupaiids the hypocone (when present) is often very low on the posterior aspect of the molar and does not occlude with the hypoconulid but instead occludes with the paraconid, paracristid, and protoconid of the following tooth. The only contact that the hypoconulid has with the upper dentition is when the metacone is drawn through the notch between the hypoconulid and entoconid as the mandible moves into centric occlusion. In the process, the metacone shears against the posterior aspect of the entocristid and the anterior aspect of the hypoconulid and paraconid of the following tooth. The development of a twinned hypoconulid and entoconid in tupaiids appears to have been convergent upon that of both mixodectids and microsyopids and probably does not indicate any close relationship between tupaiids and either of the other families. However, the relatively more buccal position of the hypoconulid in *Ptilocercus* along with the presence of a small distinct hypocone suggest that the hypoconulid-entoconid of tupaiids was originally developed in conjunction with the development of a hypocone (if *Ptilocercus* represents the primitive condition for tupaiids) and that the morphology present in tupaiines is derived. If so, the relationship between tupaiids and, in particular, microsyopids may be somewhat closer. Convergent evolution of similar functional characteristics still cannot be ruled out.

Similarities between palaechthonids and microsyopids in hypoconulid development on preliminary inspection appear to be lacking, but there are some interesting possibilities. *Palaechthon*, *Palenochtha*, and *Premnoides* (the three palaechthonine genera) seem to lack hypoconulids, except on M_3 where there is a small hypoconulid developed into a third lobe (some *Palaechthon* and *Premnoides* specimens have a small, indistinct hypoconulid lobe, normally centered, not lingual). *Plesiolestes* and *Torrejonia* have a more distinct hypoconulid lobe (on all three molars) which may be centered or lingual. *Plesiolestes problematicus* retains a postprotocingulum on upper molars and has its lower molar hypoconulids more lobate and only slightly differentiated (more so than in palaechthonines). *Torrejonia* on the other hand, particularly *Torrejonia sirokyi*, often has a distinct hypoconulid which may or may not be separated from the entoconid by a shallow notch. In addition, both species of *Torrejonia* have a less well developed postprotocingulum which does not extend to the apex of the protocone as it does in *Plesiolestes*. Interestingly, some *Plesiolestes* specimens from the Shotgun fauna, which is slightly later in time than the type sample of *Plesiolestes*, also show a more weakly developed postprotocingulum. A possible scenario can be constructed that combines a weakening postprotocingulum (along with the development of a distinct hypocone) and a strongly cuspate and twinned hypoconulid into a functional complex, culminating in *Arctodontomys*, and later developed more fully in *Microsyops*. Mixodectids are already too derived to be ancestral to microsyopids (at least concerning the hypoconulid-hypocone complex), while plesiolestines, particularly *Torrejonia sirokyi*, fit an intermediate role more comfortably.

In other lower molar features, palaechthonids are, in general, similar to *Arctodontomys*, but variation does occur. *Arctodontomys* has a variable mesoconid as do all of the Paleocene taxa except *Plesiolestes* in which a rather strong mesoconid is invariably present. All of the species have oblique cristids that join the postvallid of the trigonid rather buccally, with only *Plesiolestes* and *Palaechthon* tending to have a more lingual joining than the other genera. All of the Paleocene genera have fairly steep molar hypoflexids which may be slightly buccally extended, while in *Arctodontomys*, the hypoflexid region tends not to be buccally extended. *Arctodontomys* has a V-shaped talonid notch and rather strong entocristids which may close off the talonid slightly at its anterior base. In this feature, it most closely resembles *Torrejonia*. *Plesiolestes* and *Palaechthon* have weaker entocristids and normally have a U-shaped talonid notch (sometimes V-shaped in *Palaechthon*). *Paromomys* has a very short and weak entocristid.

Upper premolars are not very revealing, as they are not well known in most of the Paleocene taxa and remain unknown in both species of *Torrejonia*. In *Arctodontomys*, P^4 is essentially premolariform, although a small metacone may be present. In *Plesiolestes*, *Palaechthon*, and *Paromomys*, P^4 is semimolariform with a well developed metacone (weaker in *Paromomys*) and a fairly distinct paraconule (absent in *Paromomys*).

Upper molars are similar in gross morphology between *Arctodontomys* and the Paleocene taxa, but there are distinctions, especially in *Paromomys*. All taxa have rather sharp, distinct, cuspate paraconules and metaconules, except *Paromomys*, which lacks or has very weak conules. *Arctodontomys* has a fairly strong preparaconule crista that extends buccally to the parastylar region, while the postparaconule crista is essentially absent. This is similar to the condition seen in *Palaechthon*, *Torrejonia*, and *Plesiolestes*, and is probably primitive as *Purgatorius* appears to show this as well. *Paromomys* is further derived by lacking both paraconule cristae. *Arctodontomys* has a weak to absent premetaconule crista and a weak postmetaconule crista that often extends to the posterior cingulum. All of the Paleocene taxa have a weak to absent premetaconule crista, while *Plesiolestes*, *Torrejonia wilsoni*, and *Paromomys* have a weak to absent postmetaconule crista. *Torrejonia sirokyi* has a postmetaconule crista similar to that of *Arctodontomys* as it extends buccally to the metastylar region. *Palaechthon* has a strong postmetaconule crista but it does not extend very far buccally.

Arctodontomys has anterior and posterior basal cingula that do not join lingually and a buccal cingulum as well, but a weak stylar shelf. All of the Paleocene taxa except *Paromomys* share variably weak cingula on upper molars. *Plesiolestes* has weak anterior, buccal, and posterior cingula as does *Palaechthon*, while *Torrejonia* lacks or has a very weak posterior cingulum. *Paromomys* has rather well developed and broad anterior, posterior, and buccal cingula. All of the Paleocene genera lack a distinct stylar shelf except *Paromomys*, in which the stylar shelf is only slightly better developed.

The development of upper molar hypocones is variable in the Paleocene taxa, as discussed above. In *Arctodontomys*, there is no postprotocingulum and a weak hypocone is developed on the posterior flank of the protocone, on a posterior cingulum. It is not distinct and separated from the protocone by a sharp crevice. In *Palaechthon* and *Plesiolestes*, the postprotocingulum sweeps down from the apex of the protocone extending posteriorly and then turning buccally to form a small hypocone shelf on the posterior flank of the protocone. In *Paromomys*, this hypocone shelf is extended posteriorly and buccally to form a fourth, hypocone lobe. *Torrejonia* is intermediate between *Plesiolestes* and *Arctodontomys*. The hypocone is relatively larger in *Torrejonia* than in *Plesiolestes* and is slightly more distinct. It appears to be formed on a reduced postprotocingulum which does not extend to the apex of the protocone, as in *Plesiolestes*. In the Shotgun sample of *T. sirokyi* (see Chapter III), the postprotocingulum is even less extended towards the apex of the protocone and the hypocone is very similar to the one developed in *Arctodontomys*.

The question of whether *Arctodontomys* arose from some Paleocene palaechthonid is difficult to answer with the evidence available. There is no fossil evidence for palaechthonids from the last appearance of *Torrejonia sirokyi* at the Saddle Locality (late, early Tiffanian, late Paleocene) in the Bison Basin to the first appearance of microsyopids in the form of *Arctodontomys simplicidens* in the Clark's Fork Basin, Wyoming and the Piceance Creek Basin, Colorado.

Arctodontomys simplicidens appears to be more closely related to *Torrejonia* than to any other Paleocene palaechthonid, but significant differences still exist between these two taxa. *Arctodontomys* is primitive in a number of features (such as in its simple fourth premolar morphology), but there are indications that these may be secondarily derived characters that do not simply reflect primitive retentions from a *Purgatorius*-like ancestry, particularly if microsyopids are derived from palaechthonids. If so, a scenario can be constructed which views a *Torrejonia* to *Arctodontomys* relationship characterized by a simplification of premolar morphology and a change in hypoconulid and hypocone morphology from a *Plesiolestes*-like ancestor, to an intermediate form such as *Torrejonia*, to *Arctodontomys*. *Microsyops* then begins to molarize its upper and lower P4 and continues the development of hypoconulid and hypocone trends begun in *Torrejonia* and *Arctodontomys*. This could explain the different manifestations of P_4 molarization exhibited in *Plesiolestes* and *Microsyops*, a difficulty in the hypothesis of Bown and Gingerich (1973) regarding *Plesiolestes* to *Cynodontomys* (=*Microsyops*).

The late Paleocene was a cooler climatic period than either the middle Paleocene or early Eocene (see Chapter III). It is possible that the transition between *Torrejonia* and *Arctodontomys* occurred in more southern areas, with *Arctodontomys* not occurring in northern fossil assemblages until migration led it north with the warming temperatures of the early Eocene. The presence of *Arctodontomys simplicidens* in northern Colorado in the early Eocene is suggestive evidence which may support this scenario.

The hypothesis is testable if appropriate aged localities can be found in southern Wyoming, Colorado, or New Mexico. Of the known early and middle Tiffanian (later Paleocene) localities in North America, only Little Muddy Creek and Twin Creek (both fragmentary collections) from the late early and early middle Tiffanian, respectively, in southwestern Wyoming, localities from the Bison Basin (early middle to late middle Tiffanian) in south-central Wyoming, Mason Pocket (late middle Tiffanian), an isolated bone concentration from southwestern Colorado, and possibly Joes Bone Bed (late middle or late Tiffanian) in southern Texas, sample the appropriate age in southern localities. Of these, only Mason Pocket and Joes Bone Bed can be considered true southern localities. Only one palaechthonid (*T. sirokyi* from Little Muddy Creek) and one microsyopid (*Navajovius*, from Mason Pocket, Joes Bone Bed, and Twin Creek) are preserved in any of these samples. More complete samples at a greater number of early and middle Tiffanian localities, particularly in Colorado and New Mexico, are needed to truly test the above hypothesis. If the hypothesis is true, morphologically intermediate microsyopids may be found in the appropriate southern localities. Until then, the possible relationships between middle Paleocene palaechthonids and early Eocene microsyopids will have to remain tentative. At this time all that can be said is that a *Torrejonia*-like form would not be an unreasonable ancestral taxon for later *Arctodontomys*. It appears that the relationships between Paleocene palaechthonids and Eocene microsyopids is closer than is a relationship between either group and mixodectids and retention of both families in the superfamily Microsyopoidea seems warranted at this time.

MICROSYOPID-LEPTICTID RELATIONSHIPS

The basis for a possible relationship between leptictids and microsyopids is founded wholly in structures of the basicranial region, specifically those of the middle ear. Szalay (1969b) compared the middle ear of *Microsyops* closely with *Leptictis* and *Plesiadapis*, concluding that the structures of the middle ear of *Microsyops* are, "the major obstacle to an unquestioned allocation of microsyopids to the Primates." He viewed the anatomy of the middle ear of *Microsyops* as very primitive and similar to that of the primitive primate morphotype. In 1972, Szalay studied the ear region of *Phenacolemur* (see Chapter III) and began to formulate an hypothesis as to the primitive condition of the primate middle ear region. Szalay (1972) hypothesized that the primitive primate ectotympanic (see Chapter III, for discussion and illustrations of the structures of the middle ear cavity) extended from the dorsal covering of the middle ear (either cartilagenous or ossified). In 1975 Szalay added the following characters to his concept of the primitive primate middle ear: 1) a petrosal bulla; 2) loss of medial entocarotid artery; 3) a rounded promontorium; 4) bony canals surrounding all intrabullar carotid circulation; 5) the bony canal of the lateral entocarotid artery ventrally "shielding" the fenestra rotunda (cochlear fenestra). As noted above, Szalay (1976, 1977) and Szalay and Delson (1979) rejected the contention of Van Valen (1969), Bown and Gingerich (1973), Bown and Rose (1976), and Gingerich (1976) that microsyopids were primates, not only because they felt that the dental similarities were convergent between microsyopids and primates, but also that the middle ear morphology allied microsyopids more closely with leptictids and rodents.

The middle ear morphology of *Microsyops* has been described in a single specimen, AMNH 55286, a *M. knightensis* specimen from the Huerfano Formation, locality II, in Colorado. Additional cranial material of *Microsyops* which may add information concerning the morphology of this region has been reported (Eaton, 1982, Stucky, Krishtalka, Swarts, and Rose, 1985) but has yet to be described. Szalay (1969b) has thoroughly described the available skull, and I shall only summarize his description and add a few additional comments.

Figure 22 shows the ear region of AMNH 55286 and illustrates the relevant features. There is no ossified auditory bulla preserved on the specimen. The promontorium of the petrosal is rather rounded on its ventral aspect. The dorsal-medial aspect is somewhat ovoid with the long axis oriented anterior-posteriorly. The ventral-lateral surface expands somewhat laterally ventral to the vestibular fenestra. Running anterior-posteriorly along the dorsal-medial surface of the promontorium is a raised ridge of bone, the tympanic process of the promontorium, which thins slightly anteriorly. The promontorium is medially abutted quite close to the basioccipital. Between the basioccipital and the promontorium is a small canal that Szalay (1969b) has interpreted as that of the medial entocarotid artery. Butler (1956) interpreted a similar structure in *Leptictis* to represent the inferior petrosal sinus. Gingerich (1976) interpreted the canal in *Microsyops* as that of the internal acoustic meatus. As we have seen (Chapter III), the likelihood of both a medial and lateral entocarotid being present is not very high. It is unlikely that this canal represents the pathway of the medial entocarotid artery, since there is clear evidence for the presence of a lateral (or promontory) internal carotid artery (see below). It is also possible that this canal represents the pathway for an ascending pharyngeal artery as in lorises (see Chapter III) or as inferred for *Ignacius* by MacPhee, Cartmill, and Gingerich (1983). The most that can be inferred is the probable absence of a medial entocarotid artery.

The cochlear fenestra (fenestra rotunda) is positioned posterior-laterally and quite dorsally on the promontorium. The vestibular fenestra (fenestra ovale) is positioned directly lateral to and only slightly more dorsal than the cochlear fenestra. Passing just ventral to the cochlear fenestra and running anteriorly to anterior-medially around the lateral surface of the promontorium is a distinct groove for the transmission of the promontory artery. Just anterior to the cochlear fenestra, the promontory groove gives off another groove (slightly smaller) that runs dorsally to the vestibular fenestra, transmitting the stapedial artery through the stapes.

Directly posterior to the promontorium is a transversely widened foramen, the posterior lacerate foramen, while medial and slightly anterior to the promontorium is the medial lacerate foramen. Anterior and slightly lateral to the promontorium is a large fossa bounded anteriorly by the basisphenoid and alisphenoid, posteriorly by the promontorium, and laterally by the tegmen tympani. Lateral to the tegmen tympani and dorsal to the external acoustic meatus is a distinct epitympanic recess. Medial to the tegmen tympani, running anterior-laterally to posterior-medially and bounded laterally is the facial canal. It is excavated deeply into the petrosal dorsal to the vestibular and cochlear fenestrae.

There is no ossified auditory bulla preserved on the specimen. McKenna (1966) and Szalay (1969b) suggest that a partial ossified bulla was present for two reasons. First, McKenna (1966) noted the presence of a rugose portion of the petrosal, medial and ventral to the promontorium. He interpreted this as evidence that a bulla was articulated to the petrosal at this point. He noted the absence of any rugosities on either the basioccipital or basisphenoid, indicating that the bulla did not articulate with either of these elements. Second, Szalay (1969b) interpreted the presence of a tympanic process of the promontorium (petrosal) as evidence of a bullar covering. He argued that since there was no other apparent reason for this structure that it probably served as an attachment area for tissues that anchored the bulla in place. Neither of these arguments is completely satisfactory. However, a bulla of some sort was probably present. It is still possible that the covering of the middle ear was not ossified, but was cartilagenous, a possibility not ruled out by either of the two factors mentioned above. If a bulla was present, it was probably at least partially formed by an entotympanic. There was no apparent contribution from either the basioccipital or the basisphenoid, nor did the bulla completely cover the middle ear cavity. Laterally, the external acoustic meatus remained open on its ventral surface indicating that no ectotympanic tube extended from the bulla. The meatal surface of the external acoustic meatus is broken medially on both sides; thus it is impossible to determine if the ectotympanic annulus was enclosed within the bulla or was outside of it.

Szalay (1975) has stressed the similarities between the middle ear cavity of *Microsyops* and *Leptictis* in his rejection of primate status for *Microsyops*. The question of whether *Microsyops* itself was a primate or not is of little consequence, but the comparison with *Leptictis* may aid in determining character polarities of *Microsyops* ear regions.

Leptictis and *Microsyops* do share a number of features of the basicranium. Both possess a tympanic process of the promontorium that is similar in configuration. Both have posterior-laterally oriented cochlear fenestra that are ventrally traversed by the internal carotid artery. Both have

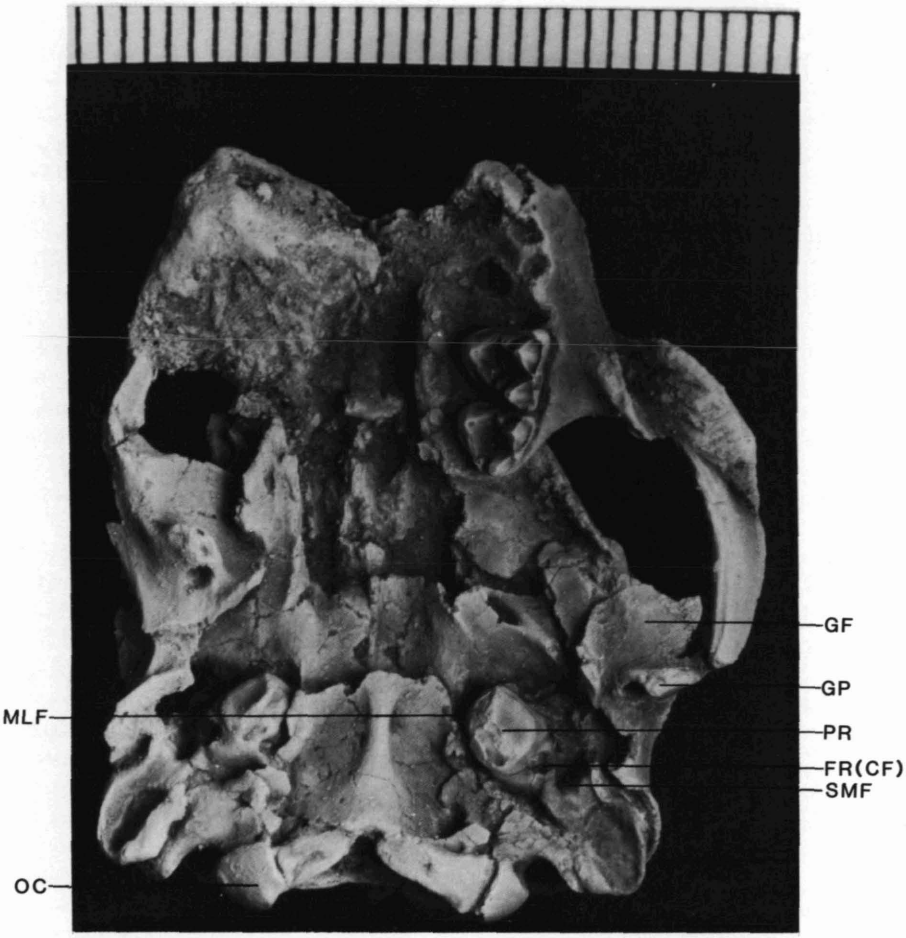

Figure 22. Basicranium and middle ear structure in AMNH 55286, *Microsyops knightensis*. Abbreviations as in Figure 14.

laterally restricted auditory bullae (if these structures are present), with the ventral surface of the external acoustic meatus open. Both have rather distinct grooves for the promontory and stapedial branches of the internal carotid artery and lack arterial bony tubes (except in the case of one *Leptictis*, see McKenna, 1966). Both have relatively large anterior fossae.

There are, however, many differences as well. *Leptictis* has very deep arterial grooves across the promontorium for the promontory and stapedial branches of the internal carotid artery, while those of *Microsyops* are shallower. The branching of the entocarotid occurs well up on the ventral aspect of the promontorium in *Leptictis*, while in *Microsyops*, the branch point occurs more laterally. In *Leptictis* the two arterial grooves are of subequal size, while in *Microsyops* the promontory groove appears larger. The promontorium is flatter dorsal-ventrally and more elongate anterior-posteriorly in *Leptictis*. There is a tympanohyal (hyoid process) roofing the facial canal ventrally in *Leptictis*, while this process is apparently absent in *Microsyops* (a well developed tympanohyal is present in *Plesiadapis*, see Chapter III). The posterior lacerate foramen is ovoid in *Leptictis* and transversely elongate in *Microsyops* (probably because it is combined with the stylomastoid foramen in *Microsyops*, while the two foramina are distinct and separate in *Leptictis*). The tegmen tympani separates the anterior fossa from the epitympanic recess in both species but is much more robust in *Microsyops*. Unlike *Microsyops*, *Leptictis* had a bullar covering which not only articulated with the petrosal (the bulla if ossified was probably of entotympanic origin in *Leptictis* as in *Microsyops*), but also clearly articulated with the alisphenoid and possibly the basisphenoid as well. There are no indications of either of these articulations in *Microsyops*. Although unknown in *Microsyops*, the ectotympanic in *Leptictis* is attached to the ectotympanic process of the medial margin of the meatal surface of the external acoustic meatus and is enclosed within the lateral margin of the auditory bulla (see Gingerich, 1976). A final difference is the posterior-lateral expansion of the petromastoid and the lack of a distinct paroccipital process in *Microsyops*.

The differences between the two genera suggest that most, if not all, of the similarities shared by them are either the result of convergent evolutionary development or, more probably, the retention of primitive characters. Examining these two taxa in the light of Szalay's primitive primate characters (ectotympanic outside the bulla, petrosal bulla, no medial internal carotid artery, rounded promontorium, bony tubes or canals for otic arteries, and ventral "shielding" of the cochlear fenestra) shows the following pattern. In *Leptictis*, the ectotympanic is not outside the bulla, but enclosed within it, there is no petrosal bulla, at least the bulla is not continuous with the petrosal, there is no medial entocarotid artery, the promontorium is not rounded, there are no bony tubes or canals, and the cochlear fenestra is partially "shielded" by a small process formed by the posterior portion of the groove for the entocarotid artery. In *Microsyops*, the disposition of the ectotympanic is unknown, there is no petrosal bulla, but it is continuous with the petrosal, there is no medial entocarotid artery, the promontorium is somewhat rounded, there are no bony tubes or canals, and the cochlear fenestra is not "shielded" by any bony projection or by the entocarotid itself.

If *Microsyops* and *Leptictis* are compared with other Paleocene and Eocene plesiadapiforms such as *Plesiadapis*, *Ignacius*, and *Phenacolemur*, and with the Eocene adapid primate *Adapis*, the following results can be seen In *Plesiadapis*, the ectotympanic is well within the bulla and is extended into an auditory tube, there is no medial entocarotid artery apparent, the promontorium is rounded, there are no bony tubes or canals for otic arteries, the bulla is well formed and continuous with the petrosal, and the cochlear fenestra is well "shielded," but not by a bony tube of the internal carotid artery. *Ignacius* appears to be very similar to *Plesiadapis*, except that there may be an ascending pharyngeal (or medial entocarotid) artery present, while *Phenacolemur* is also very similar to *Plesiadapis*. The disposition (or even the presence of) an ascending pharyngeal or medial entocarotid artery cannot be determined in *Phenacolemur*.

Adapis does not have a medial entocarotid artery, the ectotympanic is contained within the bulla, the bulla is completely continuous with the petrosal, the promontorium is rounded, there are bony tubes for the otic arteries, and the internal carotid artery ventrally shields the cochlear fenestra. *Adapis* is representative of the condition in euprimates, with variations in size of internal carotid arteries and size and extent of the ectotympanic serving to differentiate adapids and omomyids.

Comparing *Microsyops* to *Adapis*, the following differences and similarities are seen. Both lack a medial entocarotid artery (as does *Leptictis*), this character probably being primitive for plesiadapiforms and primates (perhaps for eutherians in general). Both have relatively rounded promontoria, although *Microsyops* has a less rounded one that is more similar to *Leptictis* in this character. While *Microsyops* does not (apparently) have a bulla continuous with the petrosal, it does appear to have a bulla which articulates only with the petrosal, not additionally with the alisphenoid and basisphenoid, as in *Leptictis*. *Microsyops* does not have bony tubes or canals, nor is the cochlear fenestra ventrally shielded by a bony process (the latter condition is present in *Leptictis*).

Comparing *Microsyops* with the plesiadapoid genera also shows similarities and differences. Again there is no apparent medial entocarotid (except in the case of *Ignacius*) in any of these taxa. Promontoriums are relatively rounded in all, but again less so in *Microsyops*. As in *Adapis* all of the plesiadapoids have bullae continuous with the petrosal (where this can be determined). Beyond this, plesiadapoids appear more derived than any of the other taxa. All have ectotympanics, not only contained within the auditory bulla, but extended into a tubular ectotympanic. All seem to lack any trace of an internal carotid arterial system within the bulla, although where known, the cochlear fenestra is shielded by a bony process.

If the characters are examined individually, a pattern for *Microsyops* appears. In terms of the loss of a medial entocarotid artery, this character is not restricted to primates, and is probably a primitive character retained in *Microsyops*. The development of a bulla continuous with the petrosal can easily be derived from the condition exhibited in *Microsyops* in which the bulla articulates only with the petrosal. Again this may be viewed as a primitive retention in *Microsyops* (primitive for plesiadapiforms). The rounded promontorium is probably a shared derived character of primates. The promontorium structure of *Microsyops* does not appear to be too derived from that of a primitive primate ancestor and again could well reflect the primitive condition for plesiadapiforms and primates. Bony arterial tubes or canals may be synapomorphies for primates, but also occur in other mammals (see Chapter III). Again, *Microsyops* is probably primitive in this regard. It does have grooves for the promontory and stapedial arteries and does retain both of these arteries, whereas plesiadapoids seemingly not only lack bony tubes, but also have lost or reduced the internal carotid circulation. *Microsyops* again fits a primitive ancestral position well. The same is true of the ventral shielding of the cochlear fenestra. Development of bony tubes from the condition exhibited in *Microsyops* would necessarily produce a bony covering over the ventral portion of the cochlear fenestra. Plesiadapoids may have retained this shield, even though they have lost their internal carotid circulation. Alternatively, they may have acquired this shielding independently. Finally, although there is no evidence available concerning the condition of the ectotympanic in *Microsyops*, it clearly was not extended into a tubular ectotympanic as in *Plesiadapis*. It may have been quite similar to the condition seen in *Leptictis*, which is similar to that of *Adapis*. This would suggest that an ectotympanic annulus contained within the bulla may be ectotympanic annulus contained within the bulla may be primitive for plesiadapiforms and perhaps for primates. Even if the ectotympanic of *Microsyops* is outside the bulla, this still would not argue against viewing the otic region of *Microsyops* as primitive.

In sum, *Microsyops* exhibits a suite of primitive characters in its middle ear structure. There is little or no evidence to suggest that the middle ear of *Microsyops* and *Leptictis* are similar because of shared, derived, features, but only because both retain a number of primitive eutherian characters. Older (stratigraphically) specimens of leptictids and better and older specimens of microsyopids are needed to confirm or reject this hypothesis.

MICROSYOPID ORIGINS-SUMMARY

I have examined three groups which may have been directly or indirectly involved in the origin of Eocene microsyopids: mixodectids, palaechthonids, and leptictids. I found little evidence for close microsyopid-leptictid ties. Mixodectids are similar in a number of ways to microsyopids, but differ significantly in others, and I believe their affinities lie elsewhere. Palaechthonids appear to be the best possibility for ancestry at this time. In the above discussion, I have shown features that are similar between the microsyopid *Arctodontomys* and the palaechthonid *Torrejonia*. I have discussed their differences and what is needed to test their possible relationships.

If microsyopids did not originate from a North American Paleocene group, where are their origins? At the beginning of the Eocene (about the middle Clarkforkian in North America), a fauna dominated by archaic Paleocene taxa still persisted in the North American Western Interior (Rose, 1981). The predominant groups were condylarths such as arctocyonids, phenacodontids, and hyopsodontids, archaic plesiadapiforms such as *Plesiadapis* and *Phenacolemur*, archaic carnivores such as the creodont family Oxyaenidae, true carnivores of the family Viverravidae, and pantodonts such as *Coryphodon*. At the beginning of the Wasatchian Land Mammal Age, a new fauna rapidly began to replace the old. Condylarths still dominated the fauna, but hyopsodontids began to replace phenacodontids as the dominant family, euprimates of the families Adapidae and Omomyidae replaced older primate-like taxa such as plesiadapiforms, new carnivore groups such as hyaenodontid creodonts and miacid carnivores appeared, and perissodactlys and artiodactyls appeared for the first time.

Arctodontomys first appeared in the early middle Clarkforkian but remains poorly known until the Wasatchian when its abundance in fossil assemblages increased. Appearing slightly before or at the same time as *Arctodontomys* are the tillodont *Esthonyx*, paramyid rodents, the hyopsodontid condylarth *Haplomylus*, and the pantodont *Coryphodon* (Rose, 1980, 1981a). Among these, *Haplomylus* and *Coryphodon* have probable ancestors in earlier Paleocene faunas, while rodents and *Esthonyx* were probably immigrants, either from Asia or Europe. The presence of the notoungulate, *Arctostylops* in the Clarkforkian of North America and a related genus *Palaeostylops* in Asia suggests that faunal interchange was occurring between these two continents during the late Paleocene and early Eocene (Gingerich and Rose, 1977), while the presence of rodents, *Oxyaena*, and *Coryphodon* in both Europe and North America at this time also indicates that faunal interchange was occurring between those two continents.

If *Arctodontomys* did not arise from a Paleocene taxon such as a palaechthonid, it is possible that it immigrated to North America from either Europe or Asia during the late Paleocene to early Eocene. Unfortunately there are no confirmed microsyopids known outside of North America in either Clarkforkian or Wasatchian aged sediments. McKenna (1960b) indicated that *Alsaticopithecus* from Alsace, Germany may be a microsyopid. Szalay (1969b) reviewed the evidence for the microsyopid affinities of that genus and rejected McKenna's contention, although with some reservations. Bown and Rose (1976) maintained *Alsaticopithecus* in Microsyopidae. I am unable to confirm its microsyopid affinities and believe that it may well be an artiodactyl, a conclusion also recently reached by Hooker (pers. comm.).

Russell, et al. (1967) reported a possible microsyopid from the Cuisian, late early Eocene of France. It is a single lower molar whose affinities I am unable to determine. It is a possible microsyopid, but with only a single tooth representing it, any taxonomic assessment would be extremely premature.

The possibility remains that *Arctodontomys* represents an immigrant species. However, until such time as confirmed microsyopids are found in Asia or Europe, this speculation will have to be based on negative evidence alone (the lack of a clear North American Paleocene ancestor). I believe that until such evidence becomes available, the most plausible approach is to look for microsyopid ancestors among the Paleocene taxa of North America, particularly among plesiadapiforms such as palaechthonids.

V
DIMINUTIVE MICROSYOPIDAE

In Chapter IV, I discussed the history and origins of the family Microsyopidae. That discussion focused on the larger body sized radiation of the Eocene microsyopids, the Microsyopinae. In addition to that subfamily, there is a radiation of diminutive taxa often included in microsyopids. In this chapter, I examine this radiation, including their taxonomic relationships and origins.

The diminutive taxa often included in microsyopids are *Uintasorex*, *Niptomomys*, *Navajovius*, *Berruvius*, *Tinimomys*, *Alveojunctus*, *Micromomys*, and *Palenochtha*.

All of these genera are united by their very small size (*Micromomys* and *Uintasorex* being smaller than the smallest living primate, *Microcebus*). In addition, where known, all of the genera have a microsyopid-like, lanceolate (or, at least, semi-lanceolate), procumbent lower central incisor. Russell, 1981, has recently shown that, at least, *Berruvius gingerichi* had a slightly more gracile and slender incisor, although it is still semi-lanceolate. The incisor remains unknown in the type species *Berruvius lasseroni*. This lanceolate, procumbent incisor is the major feature that unites all of these taxa with microsyopines in Microsyopidae. In addition, to a greater or lesser extent, most of the genera share the distinctive hypoconulid-entoconid twinning present in microsyopines (weak to absent in *Navajovius* and *Berruvius*, weak in *Alveojunctus*, weak to more developed in *Tinimomys*, *Micromomys*, and *Niptomomys*, and quite well developed in *Uintasorex*). In all of the genera where this characteristic twinning occurs, it is never as well developed as in microsyopines in which the notch between the hypoconulid and entoconid is much sharper and distinct. *Niptomomys* and *Navajovius* also share a laterally compressed, double rooted, blade-like upper canine with microsyopines (where known).

Recent additions to the University of Michigan collections have allowed me to re-examine certain of the relevant taxa more fully, in particular *Tinimomys* and *Micromomys*. I agree with Bown and Rose (1976) and Rose and Bown (1982) that the most reasonable course is to continue to recognize all of the above genera as microsyopids, although the inter-relationships among these taxa remain unclear.

Systematics of Diminutive Microsyopidae

Superfamily Microsyopoidea Osborn and Wortman, 1892
Family Microsyopidae Osborn and Wortman, 1892
Subfamily Uintasoricinae Szalay, 1969a

Included Genera.—Uintasorex, *Niptomomys*, *Alveojunctus*.

Emended Diagnosis.—These diminutive microsyopids are characterized by the following: 1) a single rooted (or anteriorly-posteriorly compressed, double rooted) P_3, reduced in size and much smaller than P_4; 2) weak to absent paraconids on lower molars, especially $M_{2\text{-}3}$; 3) reduced upper and lower third molars; 4) P^4 lacking a metacone; 5) upper molars lacking hypocones; 6) bulbous cusps and rather flat and wide trigon and talonid basins.

Age and Distribution.—Early Eocene (middle Clarkforkian) through middle Eocene (Uintan) of Wyoming, Utah, and Colorado.

Discussion.—The concept of uintasoricines as representing a fairly closely related group is widely accepted and I see no reason to question this opinion. They are clearly distinct from the other taxa discussed above and have been extensively reviewed and described by McKenna (1960b), Szalay (1969a), Gunnell and Gingerich (1981), and Rudman (1981).

Subfamily Navajoviinae Szalay and Delson, 1979 (new rank)

Included Genera.—Navajovius, ?Berruvius.

Emended Diagnosis.—These diminutive microsyopids can be recognized by a combination of the following characteristics: 1) P_3 double rooted, smaller than P_4, subequal in size to P_2; 2) paraconids retained, distinct and cuspidate on all lower molars; 3) upper and lower third molars reduced; 4) P^4 metacone absent; 5) upper molars with distinct hypocones; 6) cusps more acute and trigon and talonid basins rather deep and not transversely broad; 7) upper canine flattened buccal-lingually and double rooted; 8) P^3 double rooted and buccal-lingually compressed.

Age and Distribution.—Late Paleocene (middle Tiffanian), possibly early Eocene (middle Clarkforkian) of Colorado, Wyoming, Montana, and Texas (for *Navajovius*), and late Paleocene (Thanetian) of Berru and Cernay in France (for *Berruvius*).

Discussion.—*Berruvius* and *Navajovius* are both poorly known genera. They appear to be more closely related to one another than either is to any other of the small microsyopid taxa discussed above, although they both share features with uintasoricines and micromomyines (see below). *Navajovius* can be easily distinguished from uintasoricines by the presence of upper molar hypocones. Both *Berruvius* and *Navajovius* differs from uintasoricines by having distinct lower molar paraconids. *Navajovius* can also be distinguished from micromomyines by the presence of upper molar hypocones (differing in form from those of *Tinimomys*), and by having a laterally compressed, double rooted P^3. The upper dentition of *Berruvius* is still poorly known (see Russell, 1981) so that the most diagnostic features that separate navajovines from micromomyines are as yet not documented in that genus. However, *Berruvius* shares with *Navajovius* an unexpanded P_4 and a reduced M_3, which are not shared with micromomyines. *Berruvius* has a small, but distinct hypocone, although it appears to be similar to the hypocone in *Tinimomys* in being situated on the base of the tooth instead of being elevated as in *Navajovius*. It is possible that navajovines and micromomyines could be accommodated in the same subfamily. However, I believe that they are distinct enough to warrant subfamilial recognition.

Navajovius Matthew and Granger, 1921

Navajovius Matthew and Granger, 1921, p. 5; Simpson, 1935, p. 12; Szalay, 1969b, p. 275; Schiebout, 1974, p. 15; Szalay and Delson, 1979, p. 65.

Navajovius (in part), Szalay, 1972, p. 10.

Type Species.—*Navajovius kohlhaasae*.

Included Species.—Type and *Navajovius* ?mckennai.

Diagnosis.—*Navajovius* differs from *Berruvius* by retaining one less anterior tooth, by lacking or having a weak paraconid on P_4, by having somewhat less distinct paraconids on lower molars that are less anteriorly positioned than in *Berruvius*, by lacking or having a very weak metacone on P^4, and by having a more lanceolate lower central incisor.

Discussion.—The dental formula of *Navajovius* has been the subject of considerable debate in the past, as the type (and only well preserved lower jaw) specimen does not provide enough definitive evidence to answer the question of dental homologies. In their original description, Matthew and Granger (1921) interpreted the lower dental formula of *Navajovius* as 2–1–2–3, recognizing the single rooted, high crowned tooth as a canine. In 1935, Simpson suggested that this high crowned tooth (see Figure 23, and Simpson, 1935, figure 3) is not the canine but P_2, based on the fact that this tooth could not have occluded in front of the upper canine (the standard definition of a lower canine being the tooth that occludes directly in front of the first tooth in the maxillary bone, by definition the upper canine). Simpson (1935) therefore interpreted the dental formula as 1–1–3–3, recognizing Matthew and Granger's I_2 as the canine. In 1958, Gazin suggested that *Navajovius* had a lower dental formula of 1–0–3–3. I am at a loss as to how to follow Gazin's interpretation, unless he based it on figure 3 in Simpson's 1935 paper that does not show the central incisor, although its existence is mentioned in the text. Szalay (1969b) suggested a dental formula of 1–0–4–3, choosing to recognize the tooth posterior to the central incisor as P_1 and postulating the loss of a canine. However, Szalay further confused the issue by stating that yet another tooth could have been present between what he recognized as P_1 and P_2. If this was the case, then the dental formula could either be 2–0–4–3 or 1–1–4–3. Bown and Gingerich (1972) supported Simpson's interpretation of the dental formula as 1–1–3–3. Szalay and Delson (1979) have reverted to the original interpretation of Matthew and Granger (1921) and now believe the dental formula to be 2–1–2–3.

I have carefully examined the holotype (AMNH 17390) of *Navajovius kohlhaasae*, and have reached the following conclusions. First, the number of teeth anterior to P_4 is four. Directly anterior to the P_4 is a small, double rooted P_3. The crown and roots have been broken off and lost, but a bifurcated impression is preserved on the buccal side of the lingual mandibular margin denoting the presence of this small, double rooted tooth. Simpson's (1935) figure 3 shows this tooth in place in the jaw. Anterior to the P_3 is a single, stout root, vertically implanted in the mandible. It was larger than P_3 (as judged by the root and Simpson's 1935 figure). Although Simpson interprets this tooth as P_2, he had difficulty in believing that it could be larger than P_3 (but this is a condition typical of early microsyopines, see below). Anterior to this tooth (P_2) is a diastema, not another tooth root as suggested by some authors (see Szalay, 1969b). What appears as another possible tooth root is simply the broken mandible that would have extended around the roots of the teeth immediately anterior and posterior to the diastema.

Anterior to this diastema is another tooth whose crown is almost completely missing. The root for this tooth is stout, anteriorly inclined and extends posteriorly to the root of the vertically implanted tooth posterior to it. This root configuration is further evidence to suggest that there was no tooth in the diastema between these two teeth since there is little room for a third tooth root in this space unless it was a small, shallowly implanted one. This anteriorly inclined tooth was somewhat compressed transversely, appearing as an elongate oval in occlusal view. Directly in front of this tooth is an enlarged laterally compressed, procumbent, semi-lanceolate central incisor.

Three teeth exist between I_1 and P_4. P_3 is recognized by all authors, so the questionable homologies concern the two teeth between I_1 and P_3. The anterior-most of these could be I_2, P_1, or the lower canine, while the posterior one could be either P_2 or the canine. As pointed out above, this tooth could not have occluded in front of the upper canine, a point that can be demonstrated by comparing AMNH 17390 with AMNH 17399, a well preserved left and right maxilla. Further, the larger size (larger than P_3) does not preclude it from being P_2, the condition in other microsyopid genera. The conclusion that the posterior of the two teeth in question is P_2 seem well founded.

The tooth anterior to P_2 is unlikely to be P_1, as no other microsyopid or plesiadapiform except *Purgatorius* (and possibly *Palenochtha weissae*) preserves this tooth. It is either I_2 or the lower canine. A similar morphology has been recently described by Fox (1984) for *Micromomys*. *Micromomys fremdi* preserves almost identical anterior tooth morphology, except that P_2 is double rooted. Anterior to P_2 and separated from it by a diastema is a laterally compressed, anteriorly leaning tooth. Fox interprets this tooth as a canine because it is set off by a diastema (as in *Navajovius*); it is elongate and supported by a stout root (as in *Navajovius* where the root is extended back to the root of P_2), and it has a small, bilaterally compressed crown that leans anteriorly, " as if it might have occluded on the anterior side of the tooth above, as would be appropriate for a canine." In *Navajovius*, this tooth does occlude in front of the upper canine in AMNH 17399. For these reasons, I interpret this tooth as the lower canine and interpret the lower dental formula as 1–1–3–3. Therefore *Navajovius* differs from *Berruvius* by the loss of I_2 (retained in *Berruvius*, see Russell, 1981).

Navajovius kohlhaasae Matthew and Granger, 1921
Figure 23

Navajovius kohlhaasae Matthew and Granger, 1921, p. 5; Simpson, 1935b, p. 15, fig. 3–4; Szalay, 1969b, p. 278, Pl. 30, figs. 8–9, Pl. 31, figs. 1–6; Schiebout, 1974, p. 15, figs 15e-15i; Szalay and Delson, 1979, p. 65, fig. 27.

Holotype.—AMNH 17390, left mandible with I_1, P_4-M_3, right mandible with $M_{2\text{-}3}$, right maxilla with C^1, $P^{2\text{-}4}$, left maxilla with P^4-M^3.

Type Locality.—Mason Pocket, late Paleocene (late middle Tiffanian, *Plesiadapis churchilli/Plesiadapis simonsi* Lineage-Zone, Ti4), Tiffany Beds, southwestern Colorado.

Age and Distribution.—*Navajovius kohlhaasae*, in addition to the type locality, is reported from Joe's Bone Bed (Ti5), late Paleocene, late Tiffanian and Ray's Bone Bed (Ti3), late Paleocene, early middle Tiffanian, both from the Black Peaks Fauna, southwestern Texas, and from Twin Creek (Ti3), late Paleocene, early middle Tiffanian, of southwestern Wyoming.

Discussion.—Other than the type locality, none of the material attributed to *N. kohlhaasae* is very well represented. Schiebout (1974) referred three specimens (TMM 40147–62, maxilla with M^2, part of P^4 and M^3, TMM 40537–100, broken upper molar, and TMM 40537–127, a right M_1) from the early middle Tiffanian, Ray's Bone Bed level and four specimens (TMM 41365–340, left M_1, TMM 41365–500, right M_2, TMM 41365–636, and TMM 41365–697, M_2) from the late Tiffanian Joe's Bone Bed level to *N. kohlhaasae*. As she correctly pointed out, the range of morphological and size variation in *Navajovius* remains unknown. While the teeth from the Black Peaks fauna are slightly smaller, Schiebout chose to retain them in *N. kohlhaasae*, a position I fully support (see Table 10, for *Navajovius* measurements).

I take this opportunity to report a further occurrence of *N. kohlhaasae* from the early middle Tiffanian. These teeth (UM 83895, a right upper P4 (see Figure 24) and two broken right upper molars) are from the Twin Creek locality, Evanston Formation, Lincoln County, Wyoming. The material, while fragmentary, is indistinguishable from *N. kohlhaasae* and I refer it to that species.

Navajovius? *mckennai* Szalay, 1969b

Navajovius? *mckennai* Szalay, 1969b, p. 280, Pl. 30, figs. 10–11.

Holotype.—AMNH 48612, left maxilla with P^3-M^1.

Type Locality.—American Museum of Natural History Quarry 58, San Jose Formation, Regina, New Mexico.

Age and Distribution.—Early Eocene, Almagre fauna, New Mexico. Known by type specimen only.

Discussion.—Bown (1979) has suggested that this specimen represents *Niptomomys*, not *Navajovius*. P^3 is greatly reduced in *N.*(?) *mckennai* and double rooted as in *Niptomomys* and *N. kohlhaasae*, and it is also somewhat compressed transversely. *N.* (?)*mckennai* resembles *N. kohlhaasae* by having more cuspate, less bulbous cusps, by having P^4 with a distinct protocone which sweeps steeply away posteriorly (more steeply than in *N. kohlhaasae*) unlike typical *Niptomomys*. *N.*(?) *mckennai* also resembles the type species by having a distinct hypocone on M^1. Bown (1979) has claimed that *Niptomomys* has a variably present hypocone. I have been unable to confirm this, although a very small cuspule may sometimes develop on the postcingulum. In *Navajovius*, the hypocone, while not large, is always present and distinct (at least as far as sample sizes allow its confirmation). *N.*(?) *mckennai* resembles *Niptomomys* in having reduced or absent conules on M^1 and by having pre- and postprotocristae which diverge at a greater angle than is typical of *Navajovius*. As this species is only represented by a single specimen, there is little point in discussing its affinities until it becomes better known. Bown (1979) has hypothesized that *Niptomomys* may be derived from *Navajovius*. *N.* (?)*mckennai* could be viewed as tentative support for such a hypothesis and suggests that an additional lineage of small microsyopids may have existed in the early Eocene.

Navajovius sp.

Navajovius sp., Wolberg, 1979, p. 86.
Navajovius, cf. *N. kohlhaasae*, Wolberg, 1979, p. 90.

Table 10. Measurements of *Navajovius kohlhaasae* Abbreviations as in Table 1. All measurements in mm.

Tooth Position	Parameter	N	Measurement
UM 83895			
P^4	L	1	1.7
	W	1	1.8
AMNH 17390 (Holotype)			
P_4	L	1	1.5
	W	1	0.90
M_1	L	1	1.5
	W	1	1.1
M_2	L	1	1.6
	W	1	1.2
M_3	L	1	1.4
	W	1	0.90
C^1	L	1	1.1
	W	1	0.60
P^2	L	1	0.90
	W	1	0.60
P^3	L	1	0.70
	W	1	0.50
P^4	L	1	1.6
	W	1	1.6
M^1	L	1	1.4
	W	1	2.0
M^2	L	1	1.5
	W	1	2.0
M^3	L	1	1.2
	W	1	1.5
AMNH 17399			
C^1	L	1	1.2
	W	1	0.5
P^2	L	1	1.0
	W	1	0.5
P^3	L	1	0.8
	W	1	0.6
P^4	L	1	1.6
	W	1	1.8
M^1	L	1	1.6
	W	1	2.0
M^2	L	1	1.5
	W	1	1.9
M^3	L	1	1.2
	W	1	1.7

?undescribed microsyopid, near *Navajovius*, Rose, 1981a, p. 131.

Discussion.—Wolberg (1978, 1979) has described three fragmentary teeth from the Olive and Circle faunas (Ti4), late Paleocene from western Montana. These teeth (UMVP 5977, 5425, and 5955) are similar to *N. kohlhaasae* in morphological detail but are slightly larger. They may represent a new species, but are too fragmentary to be definitive.

Rose (1981a) reported the presence of four teeth of an undescribed microsyopid, near *Navajovius* from the "Big Multi Locality," early Eocene, middle Clarkforkian in the Washakie Basin, Wyoming. These teeth (two uppers, a lower central incisor, and a lower first molar) are larger than *N. kohlhaasae* and may represent a new species of *Navajovius* or a new species of *Arctodontomys*. They may also represent a new genus of microsyopid.

Berruvius Russell, 1964

Berruvius Russell, 1964, p. 124; Szalay and Delson, 1979, p. 67.
Navajovius (in part), Szalay, 1972, p. 10.

Type Species.—Berruvius lasseroni.
Included Species.—B. lasseroni and *B. gingerichi.*
Diagnosis.—Berruvius differs from *Navajovius* by retaining I_2, by having a paraconid on P_4, by having more distinct paraconids on lower molars, by having a better developed protocone on P^4, and by having a more gracile and slender, less lanceolate lower central incisor.
Age and Distribution.—Late Paleocene, Thanetian, from Berru and Cernay in northern France.
Discussion.—Szalay (1972) suggested synonymizing *Berruvius* and *Navajovius*. In 1979, Szalay and Delson again recognized *Berruvius* as a valid genus. Further evidence recently presented by Russell (1981) confirms the distinctiveness of the two genera. The two species, *B. lasseroni* and *B. gingerichi* have been adequately described and discussed by Russell (1964, 1981) and nothing of consequence can be added to his work.

Subfamily Micromomyinae Szalay, 1974 (new rank)

Included Genera.—Micromomys and *Tinimomys.*
Diagnosis.—These diminutive microsyopids have the following characteristics: 1) P^3 reduced, but triangular in occlusal outline and three rooted; 2) paraconids distinct as in navajovines, but more shelf-like with less steeply sloping paracristids, especially on M_{2-3}; 3) P_4 enlarged; 4)upper and lower M3 only slightly reduced to unreduced; 5) P^4 with small to distinct metacone.
Age and Distribution.—Late Paleocene (early middle Tiffanian) to early Eocene (early Wasatchian) of Alberta, Canada and Wyoming.
Discussion.—Fox (1984) questioned the closeness of the relationship between *Micromomys* and *Tinimomys*. He noted that the lingually continuous cingulum characteristic of *Tinimomys* upper molars is not present in *Micromomys* (but upper molars are unknown for all *Micromomys* species except the middle Tiffanian *M. fremdi*). *Micromomys* is also less bunodont than is typical of *Tinimomys*. Finally, Fox noted that the possession of an enlarged, medial incisor is not a shared and derived character, as many early primates and plesiadapiforms possess enlarged central incisors as well.

A lingually continuous cingulum with a small but distinct

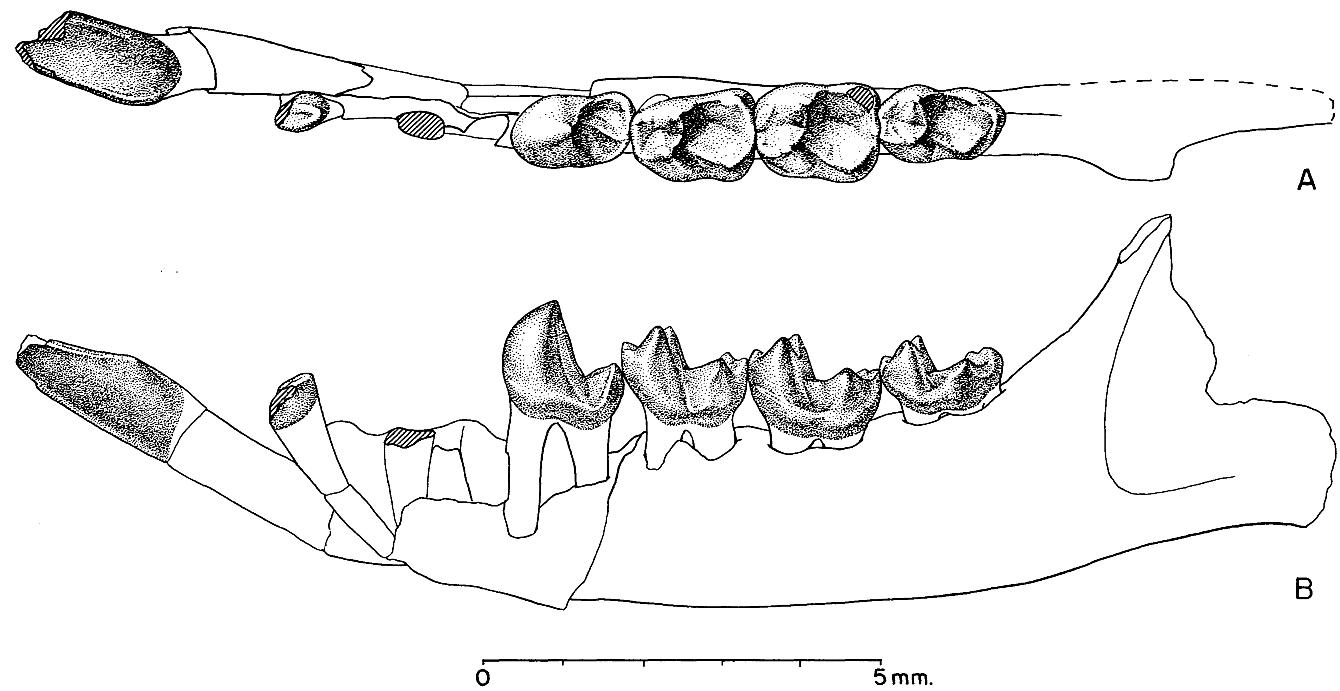

Figure 23. AMNH 17390 (Holotype), left mandible of *Navajovius kohlhaasae*. with I_1, root of C_1, alveoli for P_{2-3}, and P_4-M_3. A, occlusal view. B, lateral view.

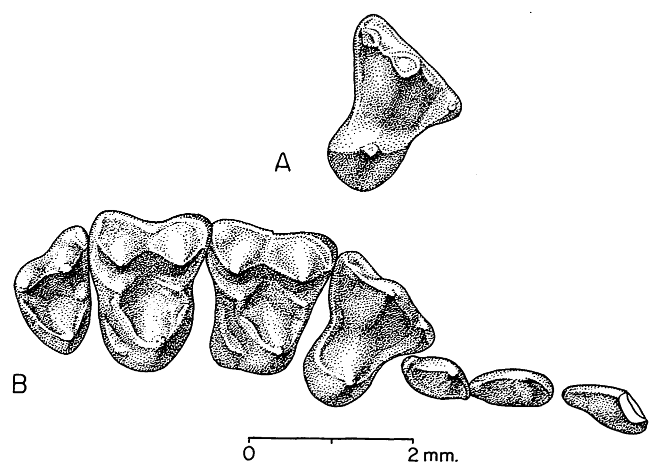

Figure 24. Upper dentition of *Navajovius kohlhaasae*. A, UM 83895, right P^4 from Twin Creek, in occlusal view. B, AMNH 17399, right maxilla with C^1, P^2-M^3, in occlusal view.

hypocone formed at the posterior-lingual border is typical of *Tinimomys graybullensis* upper molars from the Wasatchian. The cingulum is broad and continues to the buccal margin both anteriorly and posteriorly. However, in *Tinimomys* from the Clarkforkian these cingula are not as well developed. In a Clarkforkian specimen, UM 71030, the anterior and posterior cingula join very weakly on M^1 and more strongly on M^2. In neither tooth do the cingula extend buccally past the conules. In addition, this specimen has very strong conules, a condition more reminiscent of *Micromomys* than *Tinimomys*. The presence of a hypocone and larger size indicate that this specimen is *Tinimomys* and not *Micromomys*, but it can also be viewed as an intermediate stage between the upper molar morphologies typical of *Micromomys* from the middle Tiffanian and *Tinimomys* from the Wasatchian. As pointed out above, none of the younger *Micromomys* species are represented by any upper teeth so the morphology of Wasatchian *Micromomys* upper molars remains to be demonstrated.

Tinimomys (both Wasatchian and Clarkforkian species) appear to be more bunodont than *Micromomys*, but again only *M. fremdi* is represented by adequate samples. Of the other species, only three specimens with teeth other than P_4 preserved are known. These appear less bunodont than *Tinimomys* and this may be a valid generic character, but this seems a weak argument against relatively close relationships.

Concerning the lower, central incisor; while it is true that many early groups have enlarged central incisors (for example many omomyids and all plesiadapiforms except perhaps *Purgatorius*), none of them are the same morphologically. It is not only that the incisor is enlarged, but also that it is strongly compressed laterally (demonstrated below for *Micromomys* and by Rose and Bown, 1981, for *Tinimomys*), is very procumbent, and has a root that extends almost horizontally. In these features of the central incisor, *Tinimomys* and *Micromomys* share the microsyopid condition. While this may not be a synapomorphy for micromomyines, it is very likely to be a derived character shared by all microsyopoids.

Fox (1984) demonstrated that the lower dental formula of the earliest *Micromomys* species (*M. fremdi*) is 1–1–3–3. Krause (1978) had argued that an additional tooth was present in a slightly later species (*M. vossae*) based on the hypothesis that P_2 was single rooted, giving *M. vossae* a dental formula of 2–1–3–3. While still a remote possibility, it now seems much more likely that *M. vossae* also had a double rooted P_2 and thus shared the same dental formula as its likely ancestor, *M. fremdi*. Szalay (1973) described the type species of the genus *Micromomys*, *M. silvercouleei*, suggesting that its dental formula was 2–1–2–3. Bown and Rose (1976) indicated that there was another alveolus present in the type and argued for a (1–2)-1–3–3 dental formula. Krause (1978) stated that he was unable to identify any further alveoli and felt that the dental formula must be either 2–1–2–3 or 1–1–3–3, believing that only five alveoli were present anterior to P_4. Another specimen of *M. silvercouleei* (UM 77528) serves to clear up the problem. In this specimen (see Figure 25) there are clearly five alveoli between P_4 and I_1. If P_2 and P_3 are double-rooted as in *M. fremdi*, and as appears probable by the positions of the alveoli in UM 77528, then *M. silvercouleei* has the same dental formula as *M. vossae* and *M. fremdi*, 1–1–3–3. The latest species of *Micromomys*, *M. willwoodensis* is still too poorly known to determine its dental formula.

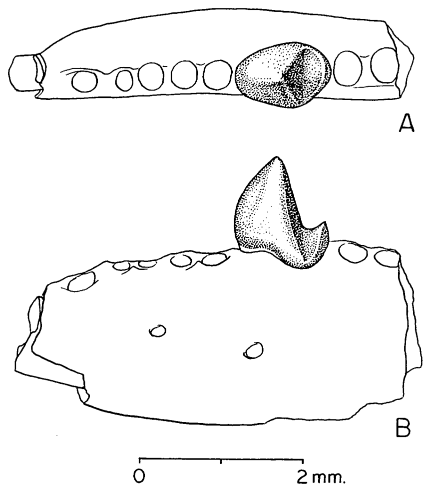

Figure 25. UM 77528, left mandible of *Micromomys silvercouleei*, with root of I_1 and P_4, and alveoli for C_1, $P_{2\text{-}3}$, M_1. A, occlusal view. B, lateral view.

Micromomys Szalay, 1973

Micromomys Szalay, 1973, p. 76; Bown and Rose, 1976, p. 135; Gingerich, 1976, p. 95; Krause, 1978, p. 1260; Szalay and Delson, 1979, p. 61; Rose and Bown, 1982, p. 64; Fox, 1984, p. 64.

Type Species.—Micromomys silvercouleei.

Included Species.—M. silvercouleei, *M. fremdi*, *M. vossae*, and *M. willwoodensis*.

Emended Diagnosis.—Differs from *Tinimomys* by being smaller, by lacking a hypocone on upper molars (where known), by having a 1–1–3–3 dental formula, by being less bunodont, by having more distinct upper molar conules, by lacking or having weak anterior and posterior cingula on upper molars, and by having a shorter, taller P_4.

Age and Distribution.—Late Paleocene (early middle Tiffanian) to early Eocene (early Wasatchian) of Alberta, Canada and Wyoming.

Discussion.—Little new information concerning *Micromomys* has been gathered and the publications of Szalay (1973), Bown and Rose (1976), Krause (1978), and Fox (1984) summarize most of the known material very well and will not be repeated here. However, two new University of Michigan specimens provide further information concerning *Micromomys* and are described below.

UM 77528 (see Figure 25), as was noted above provides evidence which demonstrates that the dental formula of *M. silvercouleei* is 1–1–3–3, the same as the earlier Tiffanian species. In addition, this specimen preserves the P_4, the alveoli of $P_{2\text{-}3}$, the lower canine, and the enlarged root of the lower incisor. The root extends back beneath the P_4 and is laterally compressed, very procumbent and enlarged as would be expected of a microsyopid. P_4 is virtually identical to that tooth in the holotype described by Szalay (1973). UM 77528 is from Schaff Quarry, late Paleocene, late Tiffanian, approximately one-half mile northeast of the type locality of *M. silvercouleei*, Princeton Quarry, which is the same age as Schaff Quarry, leaving little doubt that it represents the same species.

Of somewhat more taxonomic doubt is UM 76682 (see Figure 26), from the University of Michigan, early Wasatchian locality of SC-123. It is a left mandibular fragment preserving $M_{2\text{-}3}$. The mandible is very slender. The molars are of a typical micromomyine morphology with distinct, but laterally extended paraconids and relatively wide and deep basins. Both molars have a rather strong buccal cingulid which is common in *Tinimomys*, and variably present in *Micromomys* (present in *Berruvius* as well). The teeth are smaller than those of *Tinimomys graybullensis*, the M_2 being nearly the same size as the *M. silver-*

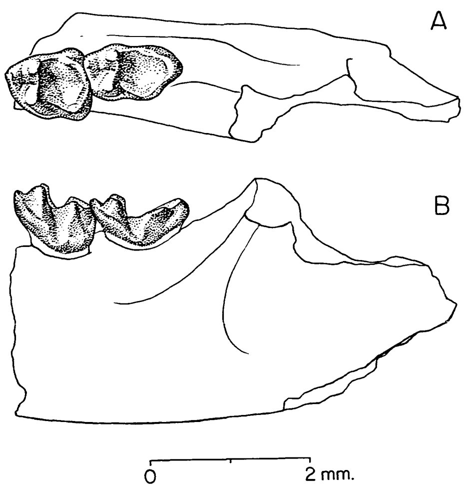

Figure 26. UM 76682, left mandible of *Micromomys*, cf. *M. willwoodensis*, with M_{2-3}. A, occlusal view. B, lateral view.

couleei type (type measures 1.1 x 1.0mm; UM 76682 M_2 measures 1.0 x .90mm). In addition, the M_3 talonid is more compressed transversely as in *Micromomys fremdi*, where the cristid connecting the hypoconulid and entoconid forms a straight line. In *Tinimomys*, this cristid is more rounded and lingually extended.

Micromomys silvercouleei is unknown from the Wasatchian, while Rose and Bown (1982) have recently described a new species of *Micromomys*, *M. willwoodensis*, from the Wasatchian. This species, represented by a mandible containing P_4, differs from *M. silvercouleei* and *M. vossae* by having P_4 about 25% larger, with a longer, broader, and taller trigonid. Rose and Bown (1982) note that the molars, judging from the alveoli, were about the same size as those of *M. silvercouleei* and *M. vossae*. *M. willwoodensis* is from the early Wasatchian, from Princeton University Camp #1 of 1928. This is equivalent to University of Michigan Sand Coulee locality SC-2. SC-2 is late early Wasatchian (Wasatchian zone Wa2 or Late Sandcouleean, see Chapter II).

UM 76682 is from Sand Coulee locality SC-123. SC-123 is slightly earlier in time than SC-2, early Wasatchian (Wa1 or early Sandcouleean) as judged by its faunal elements. Thus UM 76682 either represents the earliest occurrence of *M. willwoodensis* or the latest occurrence of *M. silvercouleei*. Although UM 76682 is rather small and fits into the size range of that expected for *M. silvercouleei*, I am inclined to assign it to *Micromomys*, cf. *M. willwoodensis*. First, because Rose and Bown (1982) note that the molars of *M. willwoodensis* were probably the same size as those of *M. silvercouleei* (or nearly so), UM 76682 is probably not out of the range of variation expected for that species. Second, for purely stratigraphic reasons, UM 76682 is more nearly the age equivalent of *M. willwoodensis*, than *M. silvercouleei*. This would have the advantage of restricting *M. silvercouleei* to the Tiffanian and *M. willwoodensis* to the Wasatchian (there are no *Micromomys* specimens known from the Clarkforkian Land Mammal Age).

Tinimomys Szalay, 1974
Figure 27

Tinimomys Szalay, 1974, p. 244; Bown and Rose, 1976, p. 126; Gingerich, 1976, p. 95; Bown, 1979, p. 72; Szalay and Delson, 1979, p. 61; Bown and Rose, 1982, p. 65.

Type Species.—Tinimomys graybullensis.

Included Species.—Type species only.

Emended Diagnosis.—Tinimomys differs from *Micromomys* by being larger, by having a hypocone and often a small pericone on upper molars, by having well developed anterior and posterior cingula on upper molars that join together lingually, by having less distinct conules on upper molars, by having a lower dental formula of 1–0–3–3, (one tooth, probably a canine, lost), by being more bunodont, and by having a longer, less elevated P_4.

Age and Distribution.—Early Eocene (middle Clarkforkian through early Wasatchian) of Wyoming, known only from the Bighorn and Washakie Basins; Rose, 1981.

Discussion.—Szalay (1974), Bown and Rose (1976), Bown (1979), Rose (1981), and Rose and Bown (1982) have figured and described most of the relevant specimens and their descriptions will not be repeated here. New University of Michigan specimens confirm the details of morphology of this genus as described by the above authors. Two additional UM specimens provide the first details of the morphology of P^{2-3}, M^3, and the ear region of *Tinimomys*, which were all previously unknown or poorly known.

UM 75602 is a right maxilla of *T. graybullensis* preserving P^4-M^3. P^4-M^2 conform to those teeth previously described. M^3 is unreduced, but differs from M^{1-2} by having a much lower metacone with a reduced metastylar region, a reduced metaconule, a weaker and more steeply sloping postprotocrista, and by having a weaker posterior cingulum which does not extend to the buccal margin of the tooth. In addition, M^3 lacks both a hypocone and a pericone. The anterior cingulum is not as broad anterior-posteriorly as is typical of M^1 and M^2. Anterior to P^4 in UM 75602 are preserved the posterior roots of P^3.

UM 85176 (from UM locality SC-327, see Figure 28) was found in a small piece of limestone. The specimen was prepared in formic acid and the following elements were extracted: a right mandible preserving P_3-M_3, two right upper teeth (P^{2-3}), a right petrosal and some assorted fragmentary bones. Because the upper and lower teeth were not found in direct occlusion it is possible that they represent different taxa and the petrosal may not be associated either. However, the upper premolars are those of a very

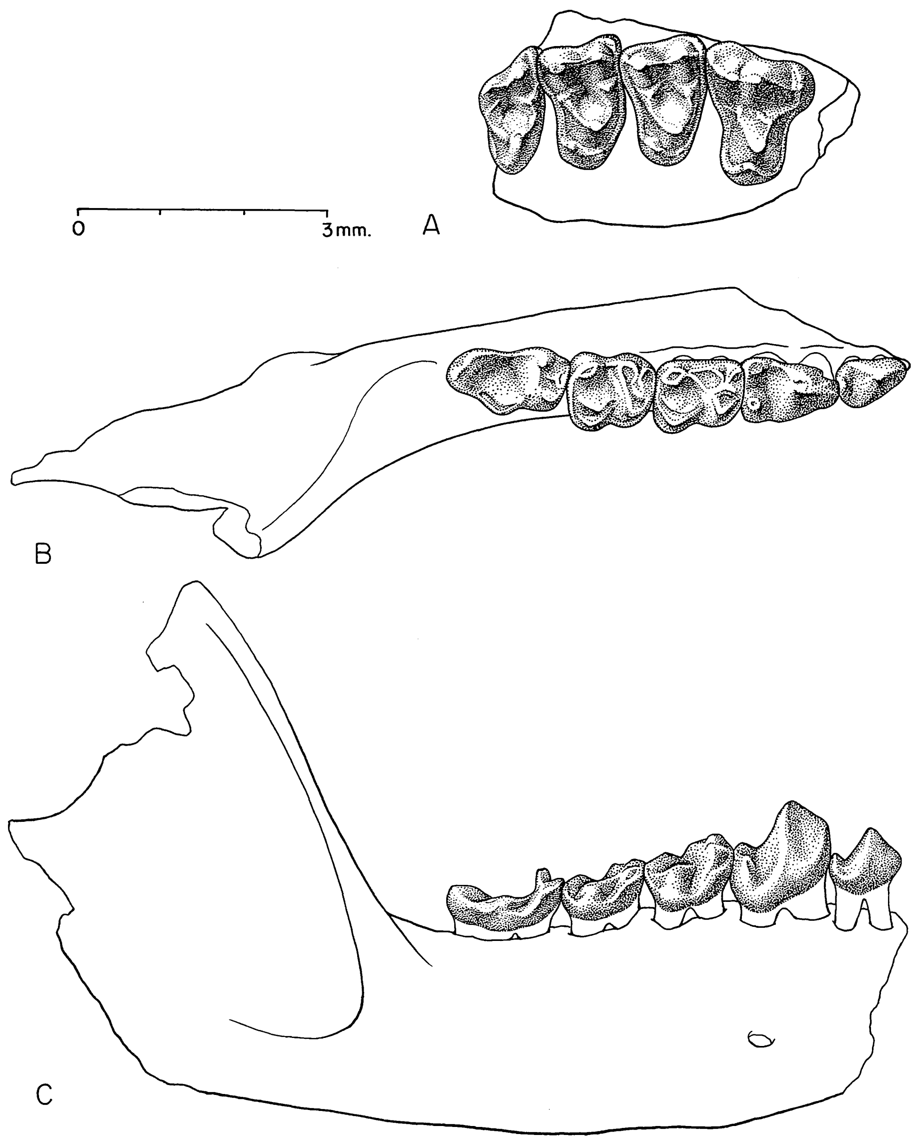

Figure 27. *Tinimomys graybullensis*. A, UM 75602, right maxilla with P^4-M^3, in occlusal view. B, UM 85176, right mandible with P_3-M_3, in occlusal view. C, same in lateral view.

small plesiadapiform, and P^3 is very similar to P^3 recently described by Fox (1984) for *Micromomys*. The petrosal is also very small and primate-like. Although the possibility of nonassociation remains, chances are not great and it is plausible that all of these elements came from the same individual. These deposits presumably represent ponds and small pools with weak to non-existent transport systems. The University of Michigan collections contain many specimens collected from limestones and none of them show signs of active transport after desiccation. This further enhances the chances that these *Tinimomys* fragments are associated. Finally, SC-327 is in the late Clarkforkian where tiny plesiadapiforms are quite scarce. *Tinimomys* is the only tiny microsyopid known from Clarkforkian sediments and the P^3 found with the *Tinimomys* mandible is quite different from that of known *Niptomomys* P^3's, making it more likely a P^3 of *Tinimomys*. The presence of these upper teeth suggests that other cranial elements were present, and supports the association of the petrosal with these dental remains.

The P^3 of *Tinimomys* (UM 85176) is quite similar to that of *Micromomys* (see Fox, 1984). It has three roots and is

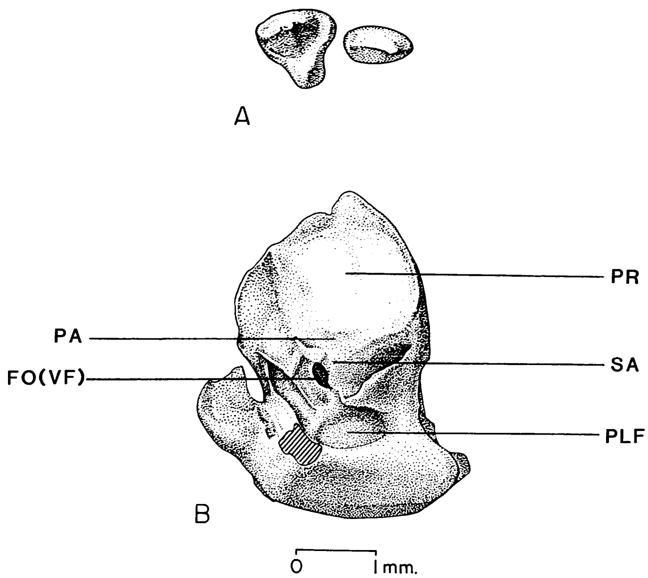

Figure 28. UM 85176, right upper P^{2-3} and right petrosal of *Tinimomys graybullensis*. A, occlusal view of P^{2-3}. B, ventral view of right petrosal. Abbreviations as in Figure 14.

triangular in occlusal outline. The paracone dominates the tooth, while the protocone is very low but expanded compared to the condition in *Micromomys fremdi*. There is a small parastyle connected to the protocone by an anterior cingulum continuous with the preprotocrista. This cingulum is infolded anterior-buccally to the protocone, dividing the tooth into buccal and lingual halves, as in P^4 of *Micromomys fremdi*. The metastylar region is also slightly better developed in *Tinimomys*, being relatively larger than in *Micromomys*. There is a small metacone cuspule low on the posterior flank of the postparacrista. The protocone also is joined to the metastylar region by a low postcingulum.

The P^2 of *Tinimomys* is two rooted and somewhat laterally compressed. There is a tall paraconid and a relatively long, sloping postparacrista which terminates at a tiny metastylar cuspule. The posterior aspect of the tooth is slightly expanded buccal-lingually. There is no trace of a protocone or a parastyle. The preparacrista is steeply angled and smoothly rounded to its base.

Measurements of the teeth are as follows: P^3 length = 1.0mm; P^3 width = 0.90mm; P^2 length = 0.85mm; P^2 width = 0.45mm.

The petrosal preserves the promontorium surrounded by small portions of the dorsal roof of the otic chamber and the mastoid region of the petrosal. The promontorium is rounded and has a prominent bulge across its ventral-medial surface which I interpret to be the tympanic process of the promontorium. On the posterior aspect of the promontorium near the dorsal border is the cochlear fenestra. The cochlear fenestra is "shielded," not ventrally as is typical of many plesiadapiforms and primates, but posteriorly by a strong wall of bone derived from the petrosal. This bony wall extends laterally to the posterior-lateral margin of the promontorium, describing a relatively deep chamber at whose posterior-medial aspect is found the cochlear fenestra. The chamber opens into the otic fossa ventrally as an elongate oval whose axis is aligned posterior-laterally to anterior-medially. The vestibular fenestra is relatively large and opens posterior-laterally. Grooves for the promontory and stapedial arteries can easily be discerned along the posterior ventral surface of the promontorium. The internal carotid artery apparently entered the otic fossa posteriorly (or perhaps slightly posterior-medially). It then continued laterally along the posterior-ventral surface of the promontorium until it nearly reached the lateral margin of the promontorium directly ventral to the lateral margin of the chamber containing the cochlear fenestra. Here it divided into a relatively large promontory branch and a somewhat smaller stapedial branch. The stapedial artery continued dorsally to the vestibular fenestra passing through the stapes. The promontory artery continued anteriorly and slightly dorsally passing between the promontorium and a distinct spinous process arising just anterior and ventral to the vestibular fenestra, and then continued around the promontorium presumably to the medial lacerate foramen (although this portion of the otic fossa is not preserved).

Directly posterior to the promontorium is a rather large posterior lacerate foramen. Posteriorly and lateral to this is a distinct paroccipital process of the mastoid. Lateral to the vestibular fenestra is a rather elongate (approximately anterior-posterior) groove, continuous anteriorly with the facial canal which continues dorsally to the internal acoustic meatus. The facial nerve exiting through the facial canal appears to have been rather small. The posterior portion of this elongate groove probably is the epitympanic recess that housed the articulations of the incus and malleus. Lateral to the epitympanic recess is a large foramen bounded posteriorly by the petromastoid wing of the petrosal and anteriorly by the petrosal roof of the tympanic cavity. Although somewhat more laterally positioned than is typical, this foramen probably is the stylomastoid foramen providing the exit for the facial nerve. Along the anterior aspect of this elongate foramen is a groove running ventrally along its surface. This may represent the stylomastoid branch of the posterior auricular artery. The mastoid region is squared-off posteriorly, but is relatively large and expanded medially.

Unfortunately, this petrosal element does not preserve any portions of the ectotympanic or bullar regions. What is preserved, however, does suggest interesting similarities with *Microsyops* (see above), as well as some differences. Szalay and Delson (1979) put *Micromomys* and *Tinimomys* in paromomyids, while Bown and Rose (1976) and Rose and Bown (1982) suggest that they belong to microsyopids. This petrosal, while very incomplete, is more suggestive of microsyopids than any known paromomyids or plesiadapids. The presence of distinct grooves on the promontorium for the promontory and stapedial arteries is very similar to the condition seen in *Microsyops*, while an apparently reduced or absent tympanic arterial system is characteristic of plesiadapoids (see Chapter III). While the pattern seen in *Microsyops* and *Tinimomys* is probably primitive, neither shows derived features which would indicate that either should be considered a plesiadapoid. The presence of a relatively large, bulbous tympanic process of the promontorium may be a shared character between *Microsyops* and *Tinimomys*, but it too may be primitive. The presence of this process suggests that *Tinimomys* had some sort of bullar covering over the tympanic cavity, but there is no indication of whether this covering was cartilagenous or ossified and, if ossified, which bony elements were responsible for its formation. While there is no evidence for the configuration of the ectotympanic, the extreme lateral position of the stylomastoid foramen suggests that the ectotympanic was not extended into a bony tube, so that the ectotympanic annulus was probably either fused into the lateral wall of an ossified bulla or was a "free" ring contained within the lateral wall of an ossified or cartilagenous bulla.

This petrosal element of *Tinimomys*, while not providing definitive proof of the affinities of the genus, is more consistent with the interpretation that *Tinimomys* was a microsyopid, than a paromomyid, either in the restricted sense of Bown and Rose (1976) or in the wider sense of Szalay and Delson (1979). *Tinimomys* differs from *Microsyops* by the more lateral position of its stylomastoid foramen (which may be the result of its extremely small size; transverse diameter of the promontorium is 0.90mm), by the posterior walling-off of the cochlear fenestra, and by the presence of a paroccipital process of the mastoid (which may also be a primitive character as it is also present in *Leptictis*, see Szalay, 1969b).

RELATIONSHIPS OF *PALENOCHTHA*

Many authors (most recently Bown and Rose, 1976, Gingerich, 1976, Bown, 1979, and Fox, 1984) have noted the similarity between palaechthonines and certain microsyopids, especially between *Palenochtha* and micromomyines. Although I have chosen to retain *Palenochtha* in palaechthonines, it is possible that it belongs to one of the diminutive microsyopid groups. Its small size and the presence of distinct paraconids on its lower molars distinguishes *Palenochtha* from the other Paleocene palaechthonines and suggests a relationship with diminutive microsyopids.

Comparing *Palenochtha* and *Micromomys* reveals a number of similarities, but a number of differences as well. The lower dental formula is the same in *Micromomys* and *P. minor*, 1–1–3–3 (*P. weissae* retains an additional antemolar tooth, perhaps P_1, see Rigby, 1980 and Chapter III). The lower molars have distinct paraconids, buccal cingulids (at least in later *Micromomys*), and broad and shallow talonid basins. Both genera also share a procumbent, laterally compressed, enlarged lower central incisor. In the upper dentition, both genera have a semimolariform P^4 with a small metacone. On upper molars, both genera have weak anterior and posterior basal cingula, prominent conules (contra Fox, 1984, who claims that *Palenochtha* has small conules), and fairly strong preparaconule and postmetaconule cristae that join the basal cingula and extend to the buccal margins of the molars.

Palenochtha and *Micromomys* differ in a number of ways. *Palenochtha* has a single rooted P_2 that is approximately the same size as the canine, while *Micromomys* has a double rooted P_2 of the same size or slightly larger than the canine. *Palenochtha* has a weak paraconid on P_4, and may have a lingually expanded P_4 talonid, and does not have the buccal aspect of the P_4 projecting below the upper margin of the mandible, while *Micromomys* lacks any trace of a paraconid, has a single cusped talonid, and the buccal aspect extends out over and below the upper margin of the mandible. P_4 in *Micromomys* is enlarged while it remains small in *Palenochtha*. *Palenochtha* has low, rather weak paracristids on its lower molars, while those of *Micromomys* are higher, shallowly sloping and extended buccally. The trigonid of the molars in *Palenochtha* is anteriorly sloping, but is much more upright in *Micromomys*. The entocristid is rather shallowly sloping in *Palenochtha* forming a V-shaped entoconid notch, while in *Micromomys* it is more steeply sloping and forms a modified U-shaped entoconid notch. In M_3 the hypoconulid is small, centered, and separated from the entoconid by a shallow notch in *Palenochtha*, while it is slightly larger and connected to the entoconid by a straight cristid in *Micromomys*. In the upper dentition, *Palenochtha* has a distinct postprotocingulum, while *Micromomys* has a weak to absent postprotocingulum, apparently formed by wear along the posterior surface of the protocone, suggesting perhaps a similar function in both genera, but still differing significantly in morphology. *Palenochtha* has a rather distinct hypocone lobe and a reduce M^3, while *Micromomys* has a small to tiny hypocone and an unreduced M^3.

Tinimomys also resembles *Palenochtha*, but differs more from that genus than does *Micromomys*. Similarities between *Tinimomys* and *Palenochtha* include: a single rooted P_2 (much more reduced in *Tinimomys*), a semimolariform P_4 (probably independently derived in both genera), and distinct molar paraconids. *Tinimomys* resembles *Micromomys* in having an enlarged P_4 (tall and relatively broad in *Micromomys*, long and relatively broad in *Tinimomys*), strong and transverse paracristids on lower molars, a more upright trigonid than in *Palenochtha* (*Tinimomys* does have trigonids more anteriorly inclined than in *Micromomys*) and broad, relatively shallow talonid basins. In the upper dentition, all three genera have a semimolariform P^4, while *Tinimomys* and *Micromomys* share a weak to absent postprotocingulum, essentially formed by a wear facet instead of a developed shelf or cristid.

Tinimomys differs from both *Micromomys* and *Palenochtha* by having a reduced lower dental formula (loss of the lower canine), a more enlarged M_3 hypoconulid with a rounded, lingually inflated cristid connecting the hypoconulid and entoconid, a more bunodont dentition, strong anterior and posterior cingula on upper molars that join lingually, more rounded, parabolic pre- and postprotocristae on upper molars, weak conules and lacking a distinct postmetaconule crista on upper molars, and a small but distinct hypocone formed on the basal cingulum. *Tinimomys* often has a pericone, as well. *Tinimomys* has an unreduced M^3 as in *Micromomys*, but differing from *Palenochtha*, which has its M^3 reduced compared to the other molars.

The presence of anteriorly inclined lower molar trigonids and a postprotocingulum both argue for the inclusion of *Palenochtha* in palaechthonids, while a number of other features discussed above suggest a relationship with micromomyines. *Palenochtha* can be viewed as a plausible ancestral morphotype for *Micromomys*, although in some respects (such as the single rooted P_2), it is too derived for direct ancestral status. *Palenochtha* seems to be more closely related to *Palaechthon* (for reasons explained in Chapter III) and I prefer to retain it in palaechthonids pending further information. If *Palenochtha* is ancestral to diminutive microsyopids, then palaechthonids as a group can be viewed as ancestral microsyopids, with palaechthonines giving rise to micromomyines, and perhaps navajovines and uintasoricines as well, while plesiolestines can be viewed as giving rise to microsyopines. This might be better reflected in classification by putting microsyopines and plesiolestines together in microsyopids and palaechthonines and the diminutive microsyopids together in another family, perhaps palaechthonids or uintasoricids. These relationships have not been convincingly established as yet, and it seems more reasonable to rely on a more horizontal classification scheme, retaining Torrejonian and early Tiffanian taxa in Palaechthonidae, and later Tiffanian and Eocene taxa in Microsyopidae, while reflecting their possible relationships by assigning both to the superfamily Microsyopoidea.

SUMMARY OF DIMINUTIVE MICROSYOPIDS

The diminutive radiation of microsyopid-like taxa remains poorly understood owing mostly to the paucity of remains that represent each taxon. The assignment of seven taxa to three subfamilies (the uintasoricines, *Uintasorex*, *Niptomomys*, and *Alveojunctus*, the navajovines, *Navajovius* and possibly *Berruvius*, and the micromomyines, *Micromomys* and *Tinimomys*) reflects their poorly understood inter-relationships. Each of the taxa involved shares features with taxa from the other two subfamilies, and a case could be made for including a taxon in a subfamily other than that which I have assigned it to. A great deal more fossil material is needed before any more definitive statements can be made concerning this group of tiny microsyopids, particularly since the relationships suggested above are based solely on dental remains and one tentatively associated petrosal element.

VI
EVOLUTIONARY PATTERNS IN MICROSYOPINAE

In an earlier chapter I dealt with the origin of Eocene microsyopids. It is apparent that this origin is still rather clouded and a definitive answer to the ancestry of microsyopids must await further fossil evidence. While the Paleocene ancestry remains poorly known, the subsequent Eocene radiation is much better documented in the fossil record. Microsyopines (including *Arctodontomys*, *Microsyops*, *Craseops*, and *Megadelphus*, n. gen.) are rare in the earliest Eocene (middle and late Clarkforkian), become better known in the early Wasatchian (Wasatchian zones Wa1 and Wa2), and by the middle to later Wasatchian (Wasatchian zones Wa3 to Wa7), become a more common member of mammalian faunas. Microsyopines remain a small, but important faunal element through the Bridgerian and survive well into the middle Eocene (Uintan Land Mammal Age).

The University of Michigan Museum of Paleontology (UM) has sent out field parties over the past twelve years to the Bighorn Basin in northwestern Wyoming, concentrating their efforts in the northern portion of that basin, specifically the Clark's Fork Basin. During that time, a large collection (over 20,000 gnathic remains) of fossil mammals and other vertebrates has been made, of which microsyopines represent about 1%. Previous to the work of the UM, additional large collections were made by Princeton University (mostly Paleocene mammals) in the Clark's Fork Basin, and Yale University (mostly Eocene mammals) in areas south of the Clark's Fork Basin. Recently, field parties from the United States Geological Survey in conjunction with Johns Hopkins University have worked in the central part of the Bighorn Basin. An additional important collection is housed in the University of Wyoming Geology Museum. What all of these collections have in common, and what makes them most useful for evolutionary study, is that each locality, from which fossil material was collected, was carefully mapped so that each one is precisely located. This may seem trivial to most field workers today, but hindsight has shown that large collections made in the past are of limited value for studying patterns of evolutionary change because precise locality records were not maintained.

Another element that makes the Bighorn Basin mammalian collections particularly important is the preponderance of badlands topography. Erosion has exposed the sediments which filled the basin along a multitude of rivers, streams, coulees, and rivulets. It is possible to trace a single sedimentary unit, often for miles, laterally. By carefully tracing these sedimentary units through a number of sedimentary sections, it is possible to build up a composite stratigraphic sequence of sediments. Combining this with precise locality information allows for placing these localities into a time-stratigraphic sequence, adding a temporal element, independent of the fossil evidence itself, to morphology. Morphological changes can then be examined through the stratigraphic section and patterns of morphological change documented through time. Any morphological feature can be examined in this manner, as well as overall patterns of morphological change. For Eocene fossils from the northwestern part of Wyoming the most abundant material consists of dental remains, and that is what I concentrate on in this section.

In the following portions of this chapter, the evolutionary history of microsyopines from the late Clarkforkian and early Wasatchian is examined in detail, concentrating on the evidence presented by the three major collections mentioned above. Preceding this discussion is a review of the systematics of early Eocene microsyopines.

SYSTEMATICS OF MICROSYOPINAE

Gunnell (1985) revised the microsyopines from the Clark's Fork Basin. I have emended that revision somewhat, and the changes are reflected below.

Order PRIMATES? Linnaeus, 1758
Suborder PLESIADAPIFORMES Simons and Tattersall, 1972
Superfamily Microsyopoidea Osborn and Wortman, 1892
Family Microsyopidae Osborn and Wortman, 1892
Subfamily Microsyopinae Osborn and Wortman, 1892

Included Genera. — *Arctodontomys*, *Microsyops*, *Craseops*, *Megadelphus* (n. gen.).

Arctodontomys Gunnell, 1985
Figures 29–31

Arctodontomys Gunnell, 1985, p. 52.

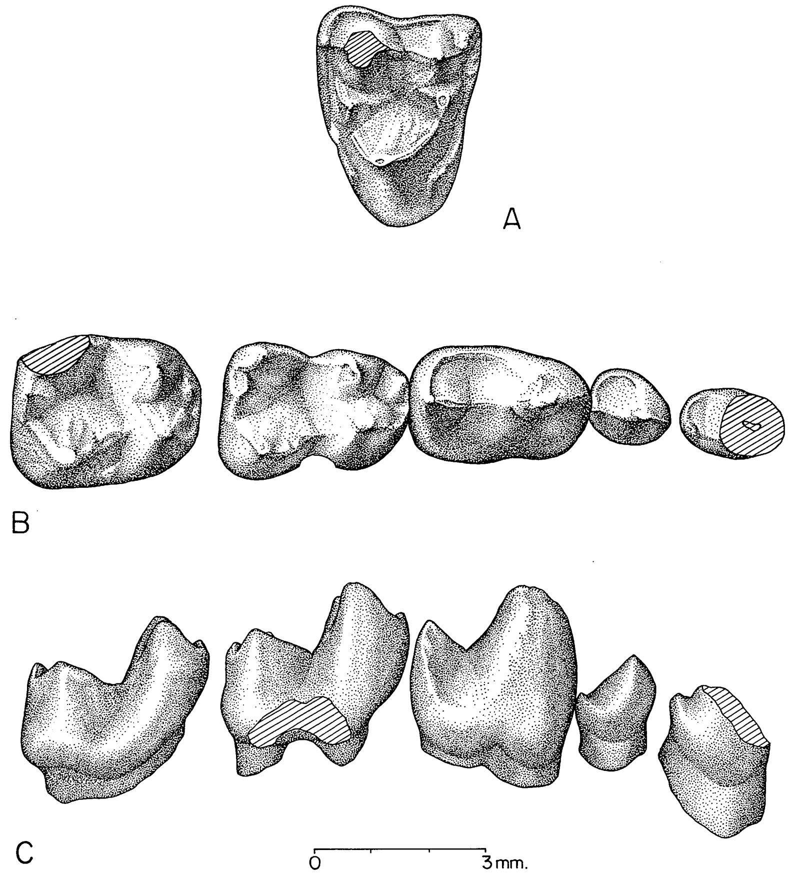

Figure 29. Upper and lower dentition of *Arctodontomys simplicidens*. A, UM 69360, left M^1, in occlusal view. B, right composite dentition (UM 67214 and UM 66178) P_2-M_2, in occlusal view. C, same in lateral view (Figure A from Gunnell, 1985, figures B and C from Rose, 1981).

Pantolestes (in part), Cope, 1882, p. 150; 1884b, p. 720.
Cynodontomys (in part), Matthew, 1915, p. 477.
Diacodexis (in part), Gazin, 1952, p. 71.
Microsyops (in part), Szalay, 1969b, p. 249; Bown and Rose, 1976, p. 122.
Microsyops, Bown, 1979, p. 67; Rose, 1981a, p. 52; Delson, 1971, p. 338; Kihm, 1984, p. 65.

Type Species.—Arctodontomys simplicidens (Rose, 1981)

Included Species.—A. simplicidens, A. wilsoni, A. nuptus.

Age and Distribution.—Early Eocene, early middle Clarkforkian (Clarkforkian zone Cf2) through middle Wasatchian (Wasatchian zone Wa3) of North America.

Discussion.—Arctodontomys was fully described and figured by Gunnell (1985) and little can be added here. Kihm (1984) reported the presence of a few fragmentary teeth of *Arctodontomys* from the Piceance Basin in northwestern Colorado. He assigned seven specimens to *A.* cf. *simplicidens* and ten specimens to *A.* near *A. wilsoni*. Based solely on his description and measurements, the assignment of the first seven to *A. simplicidens* appears doubtful as these specimens are smaller than the Clark's Fork basin sample, and suggest that their affinities may well lie with *A. wilsoni* instead. The Piceance Basin Clarkforkian fauna is not complete enough to assign localities to specific Clarkforkian intervals as defined in the Clark's Fork Basin. Consequently, the *Arctodontomys* specimens described by Kihm from the Clarkforkian may be from any part of that Land Mammal Age. Their small size and the presence of a small paracristid on P_4 suggest that these specimens may well be from the latest Clarkforkian (Cf3) and might represent early *Arctodontomys wilsoni*.

A further piece of evidence supports this interpretation. A single specimen (UM 80851) is known from the latest Clarkforkian (Cf3) from the Clark's Fork Basin. It is from

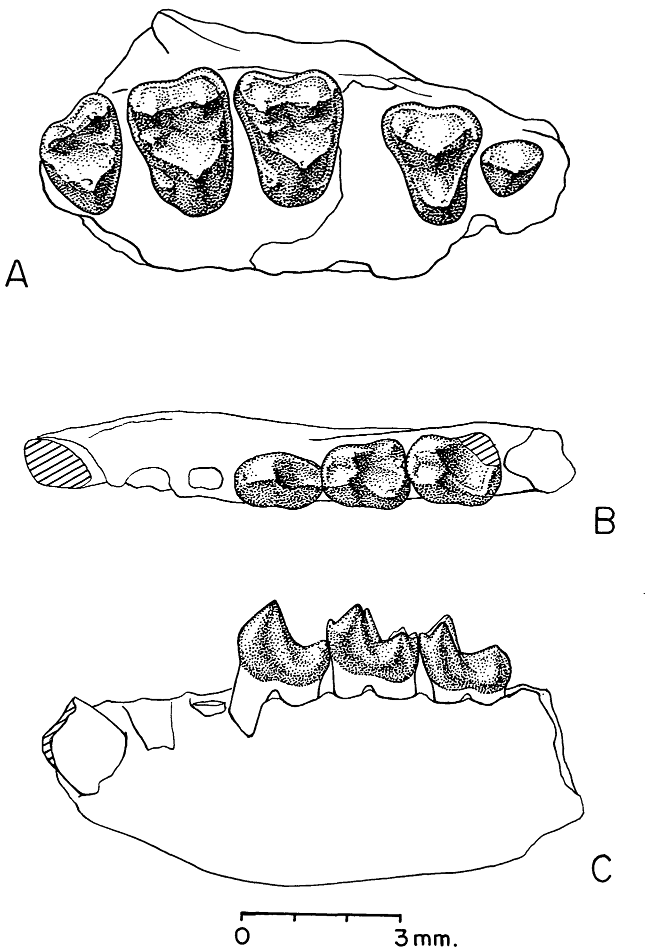

Figure 30. Upper and lower dentition of *Arctodontomys wilsoni*. A, UM 71626, right maxilla with P^3-M^3, in occlusal view. B, UM 68321, left mandible with root of I_1, alveoli for P_{2-3}, and P_4-M_2, in occlusal view. C, same in lateral view. (Figures A, B, C, from Gunnell, 1985).

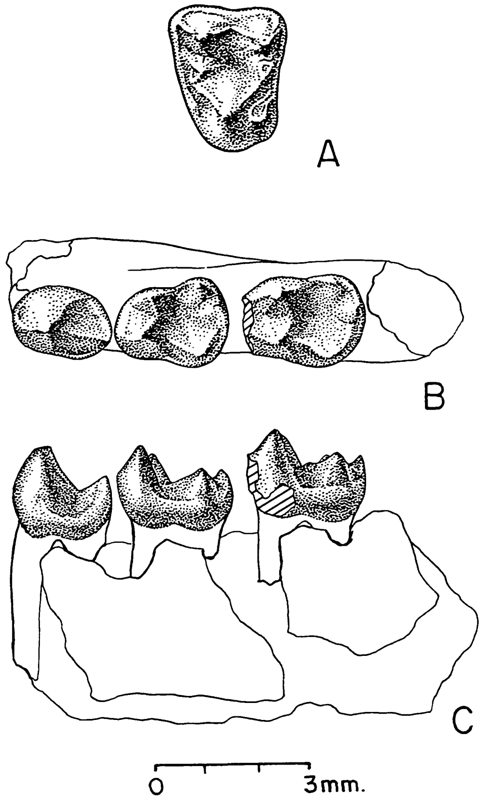

Figure 31. Upper and lower dentition of *Arctodontomys nuptus*. A, UM 82041, left M^2, in occlusal view. B, UM 66787, left mandible with P_4-M_2, in occlusal view. C, same in lateral view (Figures A, B, C, from Gunnell, 1985).

UM locality SC-71, which is 10 meters below the boundary between Cf3 and Wa0. The specimen preserves only a broken I_1 and a complete P_2 in a right portion of a mandible (see Figure 32). The mandible itself is rather shallow and gracile, which is more typical of *A. wilsoni* than of *A. simplicidens*. In addition, P_2 was approximately the same size or only slightly larger than P_3 (judging from the alveolus), which is again more typical of *A. wilsoni* than *A. simplicidens*, where P_2 is much larger than P_3. Also, P_2 is absolutely smaller than is P_2 in the type of *Arctodontomys simplicidens*. The presence of a small, *A. wilsoni*-like *Arctodontomys* species in the Clark's Fork Basin, from the very latest Clarkforkian suggests that those specimens described by Kihm as *A. simplicidens* are not that species, but are representatives of an early occurrence of *A. wilsoni*. It is possible that this latest Clarkforkian sample represents a new *Arctodontomys* species, but until sampling improves, I choose to keep both the Piceance Basin specimens and the single specimen from the Clark's Fork Basin in *Arctodontomys*, cf. *A. wilsoni*.

Arctodontomys wilsoni, except for the specimens noted above, is almost exclusively known from the early Wasatchian (Wa0 through Wa2). Only at East Alheit Pocket (McKenna, 1960b; Szalay, 1969b) in Colorado is there any indication that *A. wilsoni* occurs as late as Wasatchian zone Wa3 (see section below for a discussion of the Four Mile fauna). *A. wilsoni* has also been reported from the Piceance Basin by Kihm (1984).

Kihm (1984) describes seven specimens from the early Wasatchian DeBeque Formation from the Piceance Basin in southwestern Colorado and three specimens from the middle Wasatchian of that formation. The early Wasatchian sample is probably representative of *A. wilsoni*, although the most diagnostic tooth (lower fourth premolar) is not represented in that sample. There is an upper fourth premolar which Kihm notes has a metacone. Kihm states that this is unlike the *A. wilsoni* material described by Szalay (1969b, described as *Microsyops*) in which a metacone was lacking. Gunnell (1985), however, demonstrated that a

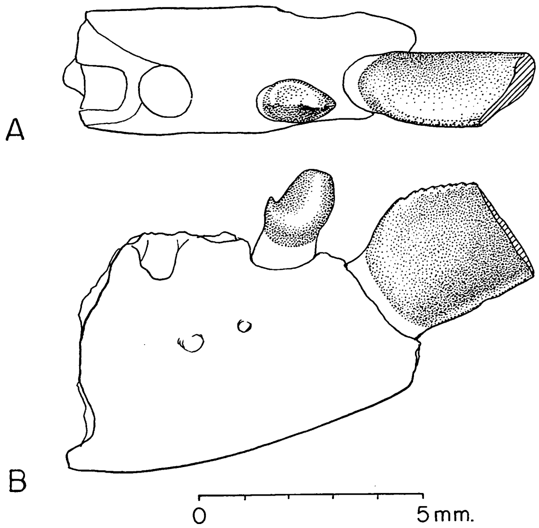

Figure 32. UM 80851, right mandible of *Arctodontomys*, cf. *A. wilsoni* from UM locality SC-71, with root of I_1 and P_2. A, occlusal view. B, lateral view.

metacone on P^4 is variable in *A. wilsoni*. The early Wasatchian sample from the DeBeque Formation conforms in known morphology and size to that for *A. wilsoni*.

The three specimens described by Kihm (1984) from the middle Wasatchian are not likely to be *A. wilsoni*. One of the specimens is a P_4 and it has a metaconid, which is not present in *Arctodontomys*, but is present in *Microsyops*. These specimens probably represent *M.* cf. *M. angustidens* (see discussion of *Microsyops angustidens* below).

Arctodontomys nuptus is a poorly known species, represented by about twenty fragmentary specimens. It is restricted to Wasatchian zone Wa3 in the Clark's Fork Basin and appears to be from equivalent aged sediments in the central Bighorn Basin. It may also be present in the Four Mile fauna of Colorado from Anthill Quarry (see Four Mile discussion below). Measurements of *Arctodontomys* specimens are provided in Table 11.

Table 11. Summary statistics of *Arctodontomys*. Abbreviations as in Table 1. All measurements in mm.

Tooth Position	Parameter	N	OR	$\bar{X}$	S	V
Arctodontomys simplicidens						
M^1	L	1		2.9		
	W	1		3.6		
P_2	L	1		1.9		
	W	1		1.2		
P_3	L	1		1.3		
	W	1		1.3		
P_4	L	2	3.0–3.2	3.10		
	W	2	2.0–2.1	2.05		
M_1	L	5	3.0–3.1	3.06	0.05	1.8
	W	5	2.2–2.3	2.26	0.05	2.4
M_2	L	1		3.5		
	W	1		2.6		
M_3	L	1		2.9		
	W	1		1.9		
Arctodontomys wilsoni						
P^3	L	2	1.6–1.8	1.70		
	W	2	1.5–1.7	1.60		
P^4	L	6	2.5–2.9	2.70	0.19	7.0
	W	6	3.0–3.4	3.25	0.16	5.1
M^1	L	9	2.7–3.3	2.97	0.18	6.0
	W	9	3.3–4.1	3.61	0.25	6.8
M^2	L	6	2.9–3.1	3.00	0.09	3.0
	W	6	3.6–4.1	3.92	0.18	4.7
M^3	L	1		2.80		
	W	1		3.00		
P_2	L	1		1.50		
	W	1		1.00		
P_3	L	1		1.70		
	W	1		1.10		
P_4	L	8	2.4–2.9	2.71	0.17	6.2
	W	8	1.6–2.1	1.85	0.17	9.1
M_1	L	17	2.7–3.1	2.84	0.11	3.7
	W	17	1.9–2.3	2.05	0.11	5.5
M_2	L	16	2.8–3.2	2.96	0.14	4.6
	W	16	2.0–2.5	2.24	0.14	6.3
M_3	L	5	3.0–3.4	3.10	0.17	5.6
	W	5	1.9–2.1	1.98	0.08	4.2
Arctodontomys nuptus						
M^1	L	1		3.6		
M^2	L	1		3.6		
	W	1		4.8		
P_4	L	1		3.10		
	W	1		2.20		
M_1	L	5	3.3–3.5	3.46	0.09	2.6
	W	5	2.4–2.7	2.52	0.13	5.2
M_2	L	4	3.5–3.8	3.63	0.13	3.6
	W	4	2.9–3.0	2.93	0.05	1.7
M_3	L	2	3.8–4.0	3.90		
	W	2		2.60		

Microsyops Leidy, 1872

Limnotherium (in part) Marsh, 1871, p. 43.

Microsyops Leidy, 1872b, p. 363; Matthew, 1915, p. 468; Stock, 1938, p. 290; Gazin, 1976, p. 8; Bown, 1982, p. A47; Lucas, 1982, p. 19; Gunnell, 1985, p. 59.

Bathrodon Marsh, 1872, p. 211.

Mesacodon Marsh, 1872, p. 212.

Palaeacodon Leidy, 1872, p. 356.

Microsyops (in part), Cope, 1881, p. 188; Szalay, 1969b, p. 248; Kihm, 1984, p. 65.

Cynodontomys Cope, 1882, p. 188; Gazin, 1952, p. 20; Gazin, 1962, p. 40; Kelley and Wood, 1954, p. 339;

McKenna, 1960b, p. 79; Robinson, 1966, P. 39; Bown and Gingerich, 1973, p. 2; Gingerich, 1976, p. 92.
Pelycodus (in part), Cope, 1882, p. 151.
Cynodontomys (in part) Matthew, 1915, p. 470.
Notharctus, Loomis, 1906, p. 283.

Type Species.—Microsyops elegans (Marsh, 1871).

Included Species.—M. elegans, M. annectens, M. scottianus, M. latidens, M. angustidens, M. kratos, M. knightensis, and *M. cardiorestes*, n. sp.

Age and Distribution.—Early Eocene, middle Wasatchian (Wa3) through late Eocene, Uintan (Ui2) of North America.

Emended Diagnosis.—Differs from *Arctodontomys* in having a metaconid on P_4, in having a better developed talonid basin on P_4, in having mesostyles on upper molars, in having a distinct to strong metacone on P^4, and in having more bulbous molar cusps. Differs from *Craseops* most notably by having a metaconule on upper molars (particularly M^{1-2}), by lacking a developed mesostylar loph on upper molars (dilambdodonty), by having a less buccally positioned hypoconid on lower P_4 and molars, and generally by having a more distinct paraconid on P_4 and lower molars with a weakly developed paracristid (also on P_3). Differs from *Megadelphus* by having a less robust I_1, and by having I^2 and C^1 laterally compressed, not reduced. Also differs from *Megadelphus* by having a double-rooted C^1.

Microsyops angustidens (Matthew, 1915)

Figure 33

Cynodontomys angustidens Matthew, 1915, p. 477, fig. 47–48.
Cynodontomys alfi McKenna, 1960b, p. 79, fig. 40.
Microsyops alfi, Szalay, 1969b, p. 255, Pl. 33, fig. 9–11.
Microsyops angustidens (in part), Szalay, 1969b, p. 255, fig. 9–11, Pl. 35, fig. 3–6, Pl. 39, fig. 5–6.
Microsyops angustidens, Gunnell, 1985, p. 60, fig. 4; Kihm, 1984, p. 69.

Age and Distribution.—Middle to late middle Wasatchian (Wasatchian zones Wa3 to Wa5) in the Bighorn Basin of Wyoming. Also known from the Piceance Basin and the Four Mile Creek area of Colorado.

Emended Diagnosis.—Microsyops angustidens differs from all later species of *Microsyops* principally by having less complex upper and lower fourth premolars, with P_4 lacking a hypoconulid. Differs from its contemporaneous sister taxon, *Microsyops cardiorestes* by being larger. Also differs from later *Microsyops* species by having variably present mesostyles (all others possess a mesostyle invariably).

Discussion.—Gunnell (1985) has described and figured this species. No additional relevant fossil material has been recovered since.

Microsyops angustidens is a difficult taxon to diagnose. As Szalay (1969b) has pointed out, it differs little from its presumed descendant species, *M. latidens*, except for its relatively less complex fourth premolar structure and its weak to absent mesostyle. It could be argued that *M. latidens* and *M. angustidens* should be synonymized. There are certain bits of information, however, that argue against this interpretation.

First, there is the presence of *Microsyops cardiorestes* in equivalent age sediments to those of *M. angustidens*. Second, there is evidence (admittedly quite poor) to suggest that there was a *Microsyops* species present earlier than either *M. angustidens* or *M. cardiorestes*. Figure 34 presents a scatter plot of tooth size scaled against stratigraphic level for the USGS sample from the Bighorn Basin in Wyoming. In sediments contemporary with *Arctodontomys nuptus* (at approximately 250 meters) are two small sized specimens, one of which has a lower P_4 preserved. This P_4 possesses a small metaconid which suggests that it is *Microsyops*, not *Arctodontomys*. This species is also present in the Four Mile fauna from Colorado (see below), represented by McKenna's (1960b) *"Cynodontomys alfi"* specimens. McKenna described *"C. alfi"* maintaining its distinction from *Microsyops angustidens* based on the "primitive" nature of *"C. alfi*'s" upper fourth premolar.

The P^4 described by McKenna as being diagnostic of the species does not belong with the first upper molar figured as being associated with it (see McKenna, 1960b, figure 40b). The M^1 has three distinct interproximal wear facets along its anterior-lateral border. The P^4 has no corresponding interproximal wear facets along its posterior-lateral border. In fact, there is no evidence of any interproximal wear along the posterior border of the P^4.

Comparison with other similarly sized Eocene mammals is inconclusive. The P^4 is superficially similar to the omomyid primate *Tetonius*, but the presence of a strong lingual cingulum and a small paraconule probably precludes its inclusion in this genus. Some *Tetonius* specimens show a weak lingual cingulum, but it does not connect the pre- and postcingula as it does in the specimen in question. Also, the specimen possesses a small metacone, which is normally absent in *Tetonius*.

The presence of a strong lingual cingulum also precludes this specimens inclusion in either *Microsyops* or *Arctodontomys*, as no species of either genus has a P^4 with a complete lingual cingulum. *Arctodontomys* species also lack a paraconule on P^4, while a paraconule is only present in later *Microsyops* species. *M. angustidens, M. latidens*, and *M. knightensis* either lack or have a very small paraconule cuspule. Later species such as *M. scottianus, M. elegans*, and *M. lundeliusi* possess paraconules on P^4; however, it is quite weakly developed in *M. lundeliusi*. P^4 in *M. annectens* is poorly known, but does appear to possess a paraconule.

Other evidence also suggests that this P^4 does not belong to *Microsyops*. UCMP 44145 (the P^4 and unassociated M^1) were found at Despair Quarry in the Four Mile Creek area.

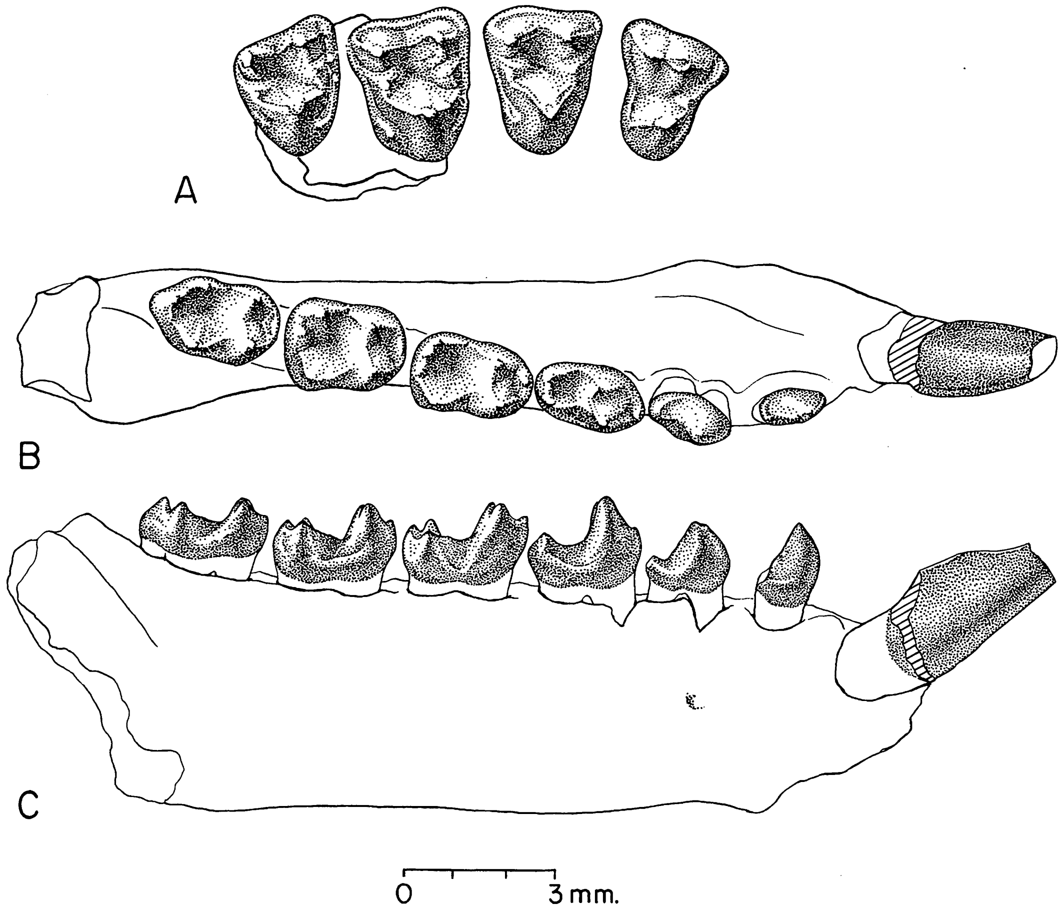

Figure 33. Upper and lower dentition of *Microsyops angustidens*. A, composite (UM 73449 and UM 76428) right maxilla with P^4-M^3, in occlusal view. B, UM 73544, right mandible with I_1-M_3, in occlusal view. C, same in lateral view (Figures A, B, C, from Gunnell, 1985).

UCMP 38340 is also a P^4 from Despair Quarry. It is very similar in all characteristics to the P^4 of *M. angustidens* described by Matthew (1915). It is not antero-posteriorly compressed, nor does it possess a paraconule or a lingual cingulum. It clearly demonstrates the presence of a *Microsyops*-like upper fourth premolar in the fauna of Despair Quarry and seriously calls into question the allocation of UCMP 44145 to that genus.

This in turn calls into question the validity of "*C. alfi*." The diagnosis of the species stands almost completely upon the supposed primitiveness of the P^4. Since it was demonstrated above that this no longer is true, it is likely that "*C. alfi*" is a junior synonym of *M. angustidens*. It is quite similar in other features to *M. angustidens*. "*C. alfi*" is slightly smaller than *M. angustidens*. The mean M_1 size for 22 specimens of "*C. alfi*" from the Four Mile area is 1.95 (ln of crown area). The mean size for 26 *M. angustidens* specimens from the Bighorn Basin is 2.15 (ln of crown area). "*C. alfi*" is about 10% smaller than *M. angustidens*. A Student t-test to determine if the two samples are statistically different was run. The two sample means are not significantly different from one another (at the 0.01 level). This supports the contention that "*C. alfi*" should be included in *M. angustidens* as a junior synonym.

It is still possible that the specimens from the Four Mile and the USGS samples represent a distinct species of *Microsyops*. They are stratigraphically older than either *M. angustidens* or *M. cardiorestes* and may be representative of the earliest immigration of *Microsyops* into Wyoming and Colorado. They are intermediate in size between *M. cardiorestes* and *M. angustidens*, but are identical (or nearly so) in morphology. I believe at present that it is most useful to retain these specimens in *M. angustidens* until more complete samples are known.

Nevertheless, these specimens represent a population that was a likely ancestor of the later two species, with *M.*

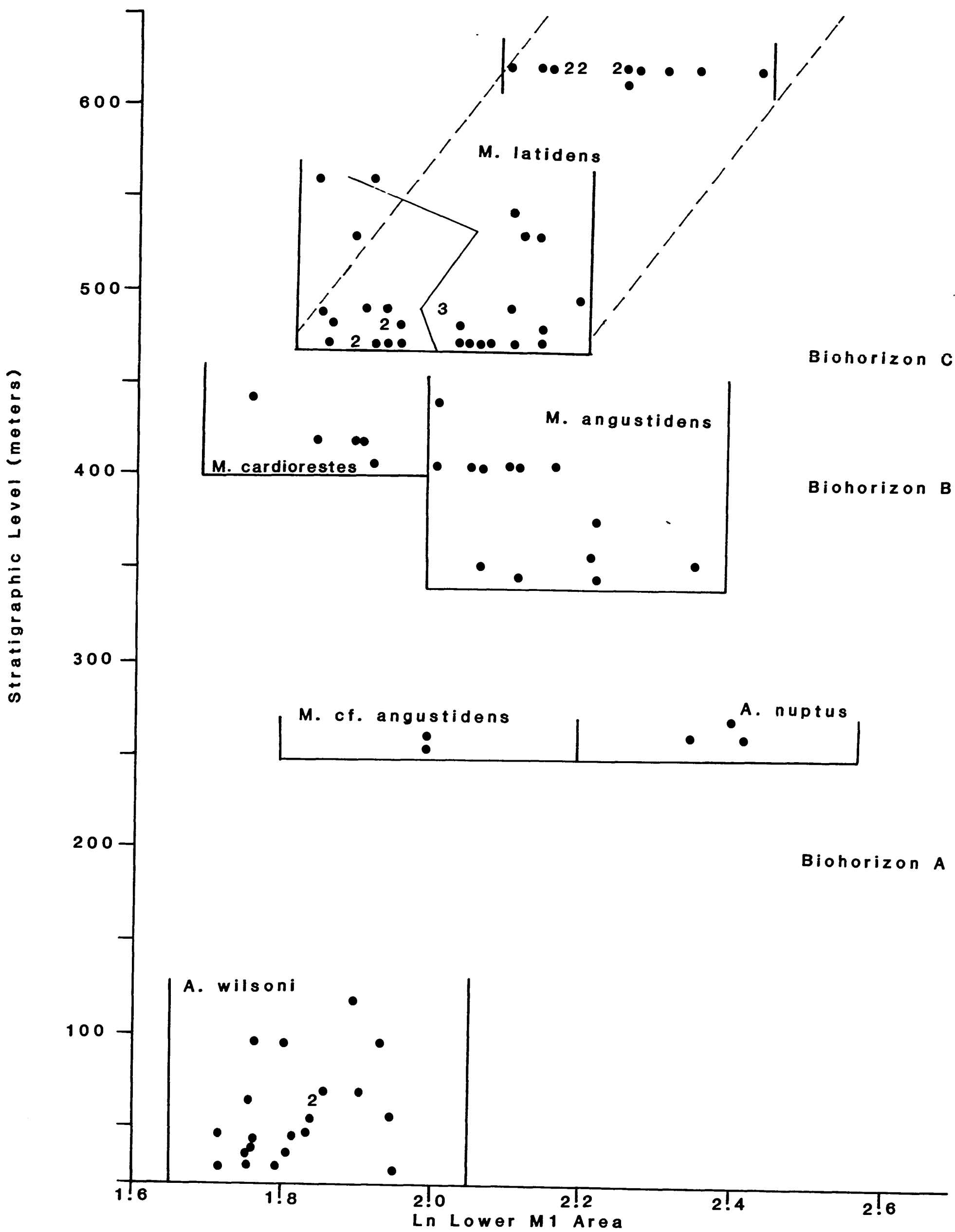

Figure 34. Plot of tooth size and stratigraphic position for microsyopine specimens from USGS sample. Abscissa represents natural log of lower first molar mean. Ordinate represent stratigraphic position in meters. Closed circles represent single specimens, while numbers represent multiple specimens of the same co-ordinates. Boxes enclose species and approximately two standard deviations on either side of species means for tooth size. Broken lines enclose one possible interpretation (as a chronocline) for size change in the *Microsyops latidens* lineage. Solid line in *M. latidens* sample connects means for each successive stratigraphic level. See text for further discussion.

cardiorestes becoming smaller and *M. angustidens* becoming larger. The presence of *M. cardiorestes* in the same stratigraphic horizons as *M. angustidens*, reinforces the need to retain *M. angustidens* as a species distinct from *M. latidens*, because it is impossible to determine at the present time, which of these two species *M. latidens* descended from. Perhaps, as sampling improves, it will be possible to determine which of the middle Wasatchian species is ancestral to *M. latidens* and at that point synonymize them as a distinct species from the other.

Another, perhaps less compelling, but nevertheless, important reason for maintaining specific distinctions between *M. latidens* and the earlier two taxa comes from biostratigraphic evidence. As was discussed in Chapter II, the Wasatchian has been divided into biochronological units based on the presence and/or absence of various taxa. Each of the boundaries for these biochronological units is representative of a major or minor faunal change within the mammalian community. The appearance of *M. angustidens* roughly coincides with the boundary between Wasatchian zones Wa3 and Wa4, while the appearance of *M. cardiorestes* coincides directly with the boundary between Wasatchian zones Wa4 and Wa5 (Biohorizon B). *M. latidens* appears coincident with the boundary between Wasatchian zones Wa5 and Wa6 (Biohorizon C). The timing of the appearance of these three *Microsyops* species suggests that they were a part of each of the three mammalian faunal events (probably immigration events, although in some cases perhaps a punctuational immigration event). This, in turn, supports the contention that each is a valid species that rapidly replaced the species previous to it. This still begs the question of ancestry but it is probable that immigrating species were descended from those species that are replaced, evolving, either by anagenesis or cladogenesis in areas unsampled by the fossil record. Table 12 presents measurements of *M. angustidens* from various samples.

Microsyops cardiorestes, new species
Figure 35

Microsyops sp. A, Gunnell, 1985, p. 62, figs. 5a-5d.

Holotype.—USGS 6598, left mandible with P_4-M_3 from USGS locality D-1452, Bighorn Basin, Wyoming.

Referred Specimens.—UM numbers 74015 (R mandible M_{2-3}), 82596 (RM_3), both from locality SC-295, and UM 75637 (L mandible M_{2-3}) from locality SC-302. USGS numbers 1375 (RM_1) from locality D-1204, 6320 (L mandible P_4-M_2), 6322 (R mandible P_4-M_1), and 6323 (L mandible P_4-M_1) from locality D-1402, and 6608 (L mandible P_4-M_2) from locality D-1454.

Age and Distribution.—Early Eocene, late middle Wasatchian, Wasatchian biochronological zone Wa5 (*Bunophorus* Interval-Zone) from the Bighorn and Clark's Fork Basins, Wyoming.

Etymology.—Kardia, Gr., heart; orestes, Gr., mountaineer, in reference to Heart Mountain, Park County, Wyoming. The first specimens of this species were discovered along the flanks of this famous gravity slide.

Diagnosis.—Differs from all other *Microsyops* species by being significantly smaller.

Description.—The only teeth known are lower P_4 and M_{1-3}. P_4 is very similar to that in *M. angustidens*. It has a prominent, tall protoconid and a distinct, but shorter, metaconid. There is a moderate paracristid that runs down the anterior flank of the protoconid turning lingually about 2/3

Table 12. Summary Statistics for *Microsyops angustidens* from various localities. Abbreviations as in Table 1. All measurements in mm. Statistics by collection.

Tooth Position	Parameter	N	OR	$\bar{X}$	S	V
AMNH *Microsyops angustidens*						
P^4	L	1		3.1		
	W	1		3.6		
M^1	L	1		3.5		
	W	1		4.3		
P_4	L	5	2.7–3.4	3.08	0.29	9.3
	W	5	1.9–2.3	2.12	0.18	8.4
M_1	L	5	3.0–3.4	3.18	0.15	4.7
	W	5	2.2–2.6	2.42	0.16	6.8
M_2	L	6	3.2–4.0	3.63	0.27	7.5
	W	6	2.5–3.1	2.70	0.25	9.3
M_3	L	1		3.30		
	W	1		2.20		
YPM *Microsyops angusidens*						
P^3	L	1		3.1		
	W	1		3.2		
M^3	L	1		3.6		
	W	1		3.5		
P_3	L	1		2.1		
	W	1		1.5		
P_4	L	6	2.8–3.4	3.10	0.23	7.4
	W	6	1.8–2.3	2.12	0.19	9.2
M_1	L	10	3.2–3.7	3.39	0.17	5.1
	W	10	2.4–2.7	2.53	0.10	3.7
M_2	L	13	3.5–4.1	3.73	0.18	4.9
	W	13	2.6–3.0	2.82	0.13	4.5
M_3	L	4	3.8–4.1	4.00	0.14	3.5
	W	4	2.3–3.0	2.55	0.31	12.2
UM *Microsyops angustidens*						
P^4	L	1		3.10		
	W	1		3.30		
M^1	L	1		3.4		
	W	1		3.7		
M^2	L	4	3.3–3.7	3.58	0.19	5.3
	W	4	3.9–4.5	4.33	0.29	6.6
M^3	L	2	3.8–4.0	3.90		
	W	2		2.60		
P_3	L	2	2.3–2.5	2.40		
	W	2		1.40		
P_4	L	10	3.1–3.6	3.34	0.16	4.9
	W	10	2.0–2.3	2.17	0.13	5.8
M_1	L	23	3.2–3.7	3.47	0.17	4.9
	W	23	2.2–2.8	2.53	0.14	5.4
M_2	L	15	3.4–3.9	3.63	0.16	4.4
	W	15	2.3–3.0	2.67	0.18	6.9
M_3	L	1		3.60		
	W	1		2.50		
USGS *Microsyops angustidens*						
M^1	L	1		3.1		
	W	1		3.7		
M^2	L	1		3.8		
	W	1		4.2		

Table 12. (Continued)

Tooth Position	Parameter	N	OR	$\bar{X}$	S	V
M^3	L	2		3.60		
	W	2	3.9–4.2	4.05		
P_4	L	6	2.9–3.6	3.18	0.25	7.8
	W	6	1.8–2.3	2.07	0.19	9.0
M_1	L	13	3.1–3.7	3.40	0.16	4.7
	W	13	2.2–2.7	2.42	0.14	5.8
M_2	L	2		3.80		
	W	2	2.6–2.9	2.75		
M_3	L	1		4.0		
	W	1		2.5		
U. California *Microsyops* cf. *M. angustidens*						
M^1	L	29	2.7–3.5	3.14	0.23	7.2
	W	29	3.4–4.2	3.79	0.22	5.9
M^2	L	26	3.0–3.6	3.33	0.13	4.0
	W	26	3.9–4.7	4.24	0.23	5.5
M^3	L	8	2.6–3.1	2.93	0.16	5.4
	W	8	3.0–3.7	3.43	0.28	8.1
P_4	L	7	2.9–3.1	2.97	0.08	2.5
	W	7	1.8–2.1	1.93	0.12	6.3
M_1	L	22	3.0–3.6	3.23	0.18	5.7
	W	22	2.1–2.6	2.33	0.15	6.2
M_2	L	13	3.1–4.0	3.48	0.28	8.1
	W	13	2.4–2.7	2.54	0.12	4.7
M_3	L	20	3.2–4.0	3.64	0.21	5.9
	W	20	2.0–2.6	2.27	0.16	7.0
U. Colorado *Microsyops* cf. *M. angustidens*						
P^4	L	1		2.70		
	W	1		3.50		
M^1	L	3	2.9–3.0	2.93	0.06	2.0
	W	3	3.2–3.9	3.57	0.35	9.8
M^2	L	1		3.2		
	W	1		4.1		
M^3	L	7	2.7–3.1	2.89	0.16	5.4
	W	7	3.0–3.6	3.31	0.22	6.6
P_4	L	2	2.7–2.9	2.80		
	W	2	1.9–2.0	1.95		
M_1	L	8	3.0–3.3	3.18	0.17	5.2
	W	8	2.2–2.4	2.29	0.08	3.6
M_2	L	7	3.2–3.5	3.33	0.11	3.3
	W	7	2.5–2.7	2.59	0.07	2.7
M_3	L	6	3.5–4.2	3.75	0.24	6.5
	W	6	2.2–2.4	2.30	0.09	3.9

of the way down. A small paraconid cuspule may develop at this inflection point. The metaconid is positioned slightly posterior to the protoconid. The talonid is much lower than the trigonid and is moderately basined. The hypoconid is well developed, while the entoconid is lower and less distinct, although present. The hypoconulid, if present at all, is very small. The oblique cristid runs anterior-posteriorly between the hypoconid and the buccal surface of the postvallid. A weak buccal cingulid may be present.

The lower first molar morphology is very similar to that of all other *Microsyops* species. The protoconid and metaconid are rather bulbous and rounded and are of subequal height. The paraconid is smaller, lower, and centered on the anterior aspect of the tooth. There is a short paracristid joining this cusp with the anterior flank of the protoconid. The trigonid is inclined slightly anteriorly and is smaller in overall proportions than the talonid. The talonid has distinct hypoconid and entoconid cusps and a small hypoconulid appressed to the base of the entoconid, separated from that cusp by a rather shallow notch. The oblique cristid joins the postvallid buccal of center and may have a small mesoconid developed on its anterior aspect. The basin is relatively broad and shallow. The entocristid is relatively steeply sloping. Weak buccal and postcingulids are present. M_2 differs from M_1 only in its slightly larger size, its more anterior-posteriorly compressed trigonid, and its less well developed paraconid, but slightly longer paracristid.

M_3 is similar to the other molars except that it is slightly reduced. It has an expanded hypoconulid that forms a third section of the talonid and is more centered on the tooth. The buccal cingulid is shorter than in the other molars and there is often a stronger mesoconid developed on the oblique cristid. The paracristid is extended buccal-lingually and the trigonid is compressed anterior-posteriorly more than in M_2.

The rest of the lower dentition is only represented by alveoli. P_3 was double rooted and smaller than P_4. P_2 was single rooted but judging from the size of the alveolus may have been nearly as large as P_3. The root of I_1 is compressed buccal-lingually as in other *Microsyops* species, and this tooth was clearly procumbent. The root appears to extend posteriorly, at least, to the posterior root of P_4.

The mandibles are quite slender and gracile. The mandibular symphysis is unfused and there is a mental foramen beneath the posterior root of P_3. An additional mental foramen may be present below the root of P_2. Measurements of *M. cardiorestes* are presented in Table 13.

Discussion.—Microsyops cardiorestes is restricted in its occurrence, for the most part, to Wasatchian biochronological zone Wa5. It first appears at the boundary between Wa4 and Wa5 (Biohorizon B) and is present throughout Wasatchian zone Wa5. *Microsyops cardiorestes* is still poorly known morphologically and stratigraphically, but it appears to be a good index species for Biohorizon B and Wasatchian zone Wa5.

M. cardiorestes appears suddenly in the fossil record at Biohorizon B. Its appearance probably represents an immigration event, although rapid phyletic evolution within the community cannot be ruled out.

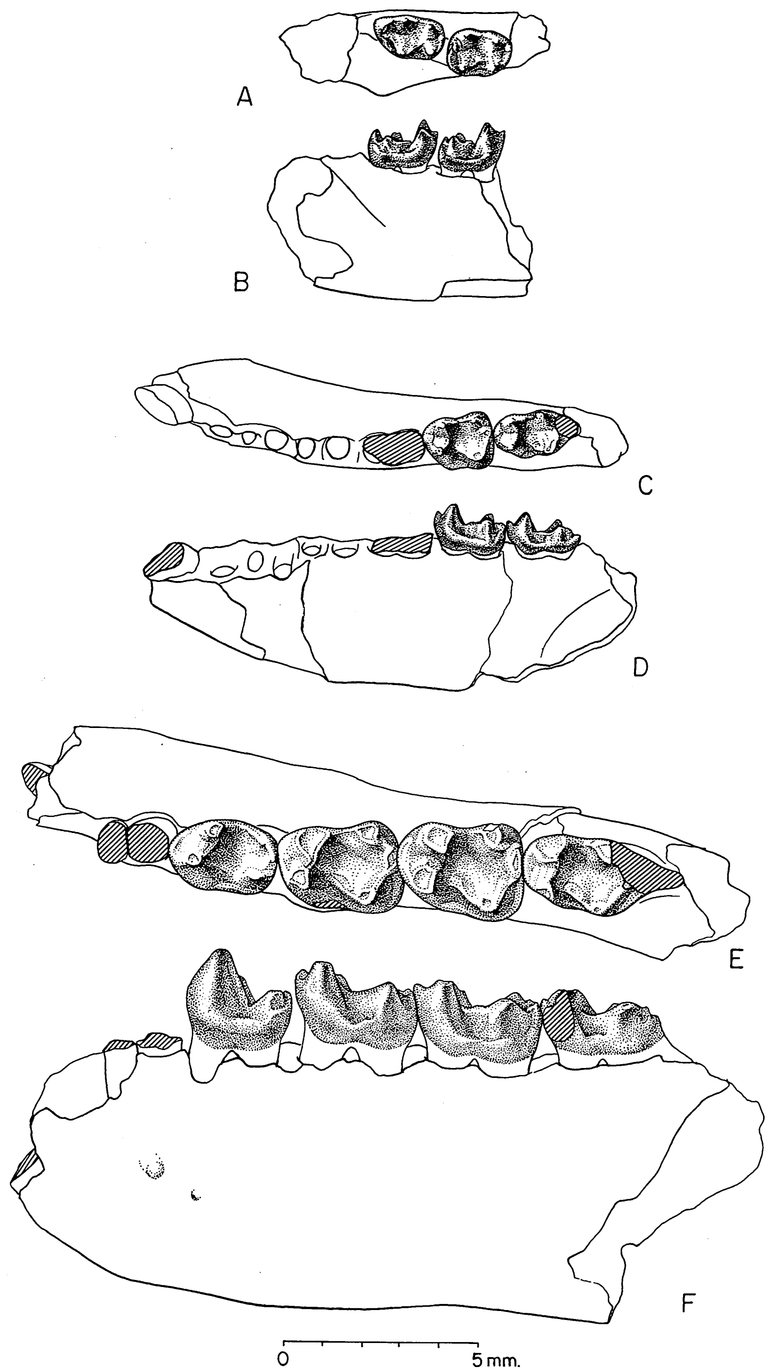

Figure 35. Lower dentition of *Microsyops cardiorestes*. A, UM 74015, right mandible with M_{2-3}, in occlusal view. B, same in lateral view. C, UM 75637, left mandible with root of I_1, alveoli for P_2-M_1, and M_{2-3}, in occlusal view. D, same in lateral view. E, USGS 6598 (Holotype), left mandible with P_4-M_3, in occlusal view. F, same in lateral view (Figures A-D from Gunnell, 1985).

Table 13. Summary Statistics for *Microsyops cardiorestes* Abbreviations as in Table 1. All measurements in mm.

Tooth Position	Parameter	N	OR	$\bar{X}$	S	V
P_4	L	5	2.5–2.9	2.72	0.18	8.1
	W	5	1.6–1.9	1.78	0.11	6.2
M_1	L	6	2.9–3.1	3.00	0.09	3.0
	W	6	1.9–2.3	2.17	0.15	6.9
M_2	L	3	2.8–3.4	3.10	0.30	9.7
	W	3	2.1–2.5	2.33	0.21	8.9
M_3	L	2	3.2–3.3	3.25		
	W	2	1.9–2.1	2.00		

Microsyops latidens (Cope, 1882)
Figure 36

Cynodontomys latidens Cope, 1882, p. 151; 1884, p. 244, Pl. 24, fig. 2; 1885, p. 456, fig. 10; Matthew, 1915, p. 473, fig. 44–46; Osborn, 1902, p. 208, fig. 35.
Pelycodus angulatus Cope, 1882, p. 151; 1883b, p. 231.
Chriacus pelvidens Cope, 1883a, p. 80; 1883b, Pl. 24e, fig. 4–4c.
Notharctus palmeri Loomis, 1906, p. 283, fig. 7a-7b.
Notharctus cingulatus Loomis, 1906, p. 284, fig. 8a-8b.
Microsyops latidens (in part), Szalay, 1969b, p. 258, Pl. 34, fig. 1–3, Pl. 35, fig. 1–2, 7–8, Pl. 36, fig. 1–2.
Cynodontomys knightensis (in part), Robinson, 1966, p. 39.

Holotype.—AMNH 4195, right mandible with M_{1-2} and left mandible with P_4, from probable Lysite equivalent beds, Wasatchian zone Wa6, Bighorn Basin, Wyoming. Found by Jacob Wortman in 1881 south of the village of Otto, Wyoming.

Age and Distribution.—Early Eocene, early late Wasatchian (Wa6, Lysitean, *Heptodon* Interval-Zone) from the Bighorn Basin, Wyoming. Also known from various other areas in Wyoming, Colorado, and New Mexico, all presumably of Lysitean (Wa6) age.

Discussion.—While earlier species of *Microsyops* and *Arctodontomys* are relatively low in abundance, *M. latidens* is known from hundreds of specimens from the Bighorn and Wind River Basins in Wyoming. By the late Wasatchian *Microsyops* has become a relatively common element in the mammalian fauna. Collections from the central Bighorn Basin (from YPM and USGS) contain large samples of *M. latidens* that provide information concerning morphology and patterns of species level evolution.

M. latidens is one of the best known species of *Microsyops*. Most of its dental morphology has been previously described and figured (see Szalay, 1969b). However, certain aspects of its upper dentition have remained unknown until now. USGS 9194 (Figure 36) preserves a virtually complete upper dentition. It shows that the probable upper dental formula was 2–1–3–3, as it is in *Megadelphus lundeliusi* (but see Chapter VII), the only other microsyopid species in which the upper anterior dentition is known.

The anterior-most upper incisor (I^1) is preserved in place in the premaxilla. Szalay (1969b) described an I^1 which he attributed to *M. latidens*, although it was an isolated tooth. The morphologies of the two teeth are quite similar and it is probable that the tooth described by Szalay is an I^1 of *M. latidens*. I^1 in USGS 9194 has a pointed crown and a rather robust root, both of which are transversely compressed. The anterior and buccal aspects are somewhat broken, obscuring the morphology of these areas. A rather prominent bulge is present on the lingual surface running the height of the tooth, bulging more prominently towards the root. Although the anterior portion of the tooth is somewhat broken, a portion of a very distinct anterior ridge, which presumably ran the anterior height of the tooth, is preserved. This gives the tooth a rather triangular outline when viewed occlusally. A sharp crest runs posteriorly from the apex and a small concavity is formed between the lingual bulge and this crest on the posterior-lingual surface of the tooth. A distinct wear facet is formed along the posterior lingual portion of the lingual bulge.

I^2, previously unknown, is a smaller version of I^1 with some minor differences. I^2 does not bulge as much lingually as I^1, and consequently appears slightly more transversely compressed than I^1. There is only a small posterior-lingual concavity and the crest running posteriorly from the apex is more steeply sloped towards the root than in I^1. The anterior ridge is less differentiated from the tooth surface than in the central incisor, but extends down the anterior surface and turns lingually near the base of the crown. It is probable that the anterior ridge of I^1 also followed this pattern.

The upper canine is broken in USGS 9194 so that its crown remains unknown. What is preserved shows that the canine was double-rooted and very laterally compressed and blade-like (as it is in all *Microsyops* species where this tooth is known). It is impossible to determine if there was a small alveolus between the canine and I^2 as there is in *M. elegans* because the premaxilla has been pushed somewhat posteriorly and dorsally.

In addition to adding morphological detail, the samples from YPM and USGS provide information about the evolutionary development of *M. latidens*. Figures 34 and 37 show the *M. latidens* samples from USGS and YPM, respectively, with tooth size (M_1 area) plotted against stratigraphic position. In the YPM sample, where specimen numbers are the largest, the means for each stratigraphic interval are connected by a solid line. At Biohorizon C, mean M_1 area is 2.06 on a natural log scale. As means are traced up the stratigraphic section there is a trend towards slight size increase, followed by a small decrease, followed by a more marked increase, immediately followed by a marked decrease in mean first lower molar size. In the USGS sample, a similar trend is seen with means staying

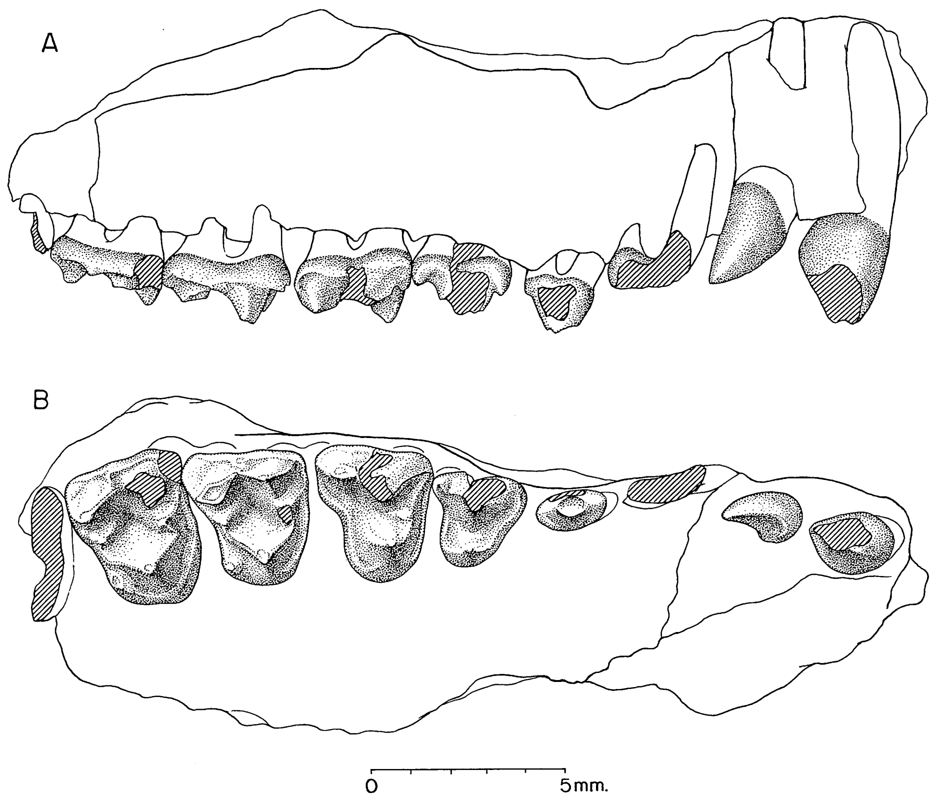

Figure 36. Upper dentition of *Microsyops latidens*. A, USGS 9194, right maxilla with I^1?-M^3, in occlusal view. B, same in lateral view.

at about the same level through three horizons, then followed by an increase in size, immediately followed by a size decrease. Later in the section, size has increased again. Although sample sizes are smaller in the USGS section, the same general pattern holds for both samples.

In addition to molar size, *M. latidens* exhibits some changes in morphology through these sections. Lower fourth premolar morphology changes through the sections. In the lower horizons just above Biohorizon C, P_4 is rather gracile with a buccal-lingually narrow talonid and a rather small hypoconulid that is often appressed to the hypoconid (differing from *M. angustidens* in which the hypoconulid is normally absent or very small). As *M. latidens* is traced up the stratigraphic section, the talonid basin of P_4 becomes somewhat broader and the hypoconulid becomes more centrally placed on the posterior aspect of the talonid. Near the top of the section, a number of specimens have P_4's with very broad talonids and hypoconulids that are now appressed to the entoconid, as in *M. scottianus*. In conjunction with this broadening of the talonid basin, the oblique cristid becomes more angled. In the lower part of the section, the oblique cristid is nearly aligned anterior-posteriorly, while near the top of the section it is angled anterior-lingually to posterior-buccally. At the top of the section, P_4 is also normally more robust with bulbous cusps. Figure 38 shows the changes in P_4 morphology in *Microsyops*.

Other morphological character changes can be noted through the stratigraphic horizons of the *Microsyops latidens* range. At the lower end of the stratigraphic range, all of the specimens tend to be gracile with small mesostyles and weak stylar shelves on upper molars and weak and restricted cingula on upper and lower molars. Nearer the top of the stratigraphic range, the gracile form remains, but, in addition, there is a more robust form with strong mesostyles and stylar shelves and very strong cingula on upper and lower molars (often extending completely around upper molars). These robust forms are more bunodont than the gracile form.

Microsyops latidens is a variable species, both in morphology and size. The more gracile, less progressive (in terms, especially, of P_4 morphology) forms resemble later *Microsyops knightensis*, while the more robust, more progressive forms resemble later *Microsyops scottianus*.

In the *M. latidens* samples from YPM and USGS, each

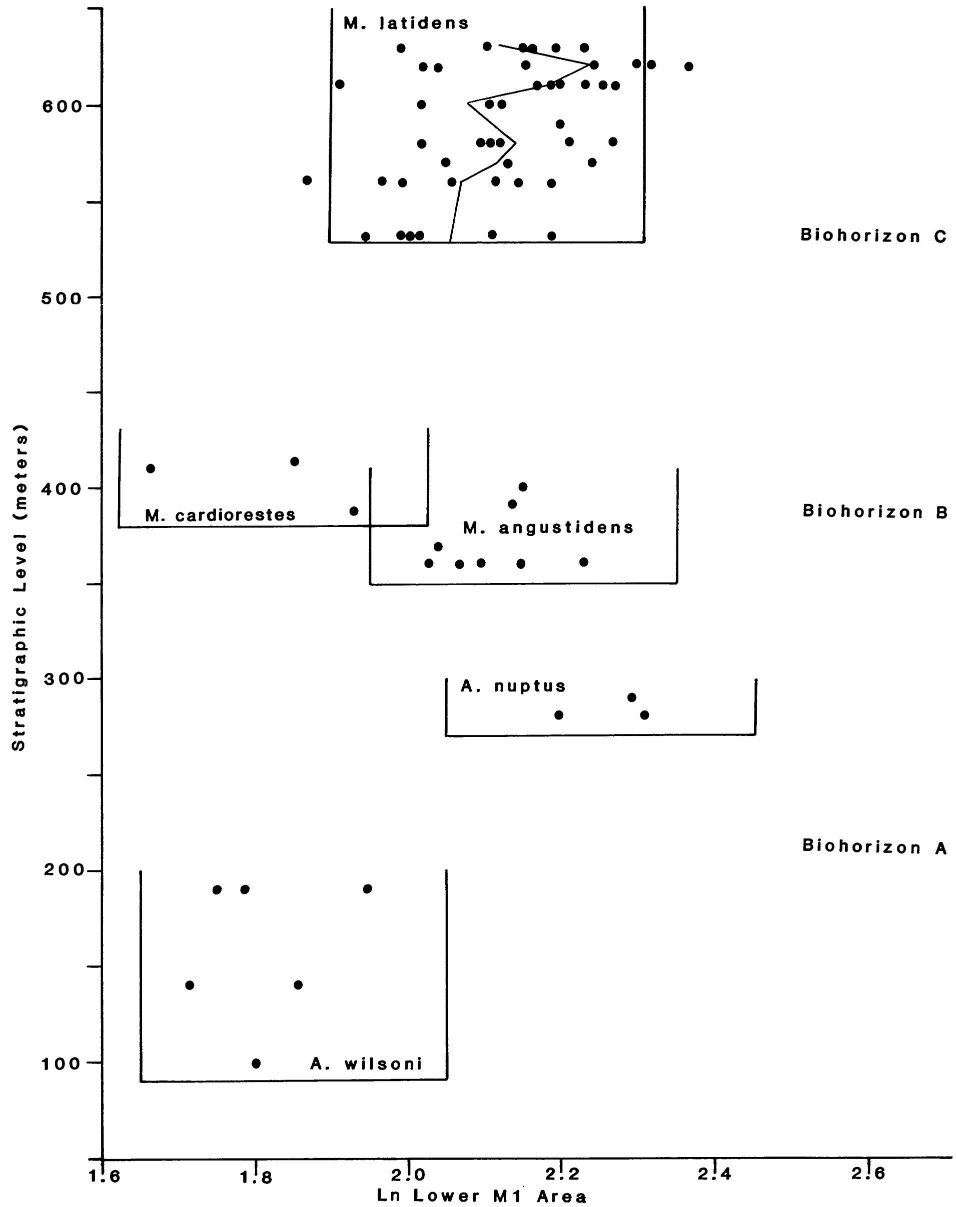

Figure 37. Plot of tooth size and stratigraphic level for the YPM microsyopine sample. Abscissa represents natural log of lower first molar area. Ordinate represents stratigraphic level in meters. Solid circles represent single specimens, while numbers indicate multiple specimens with the same co-ordinates. Boxes enclose species and approximately two standard deviations on either side of species means for tooth size. Solid line through *Microsyops latidens* sample connects means for each successive stratigraphic horizon within lineage. See text for further discussion.

stratigraphic interval of 10 meters probably represents between 40–60,000 years. This scale is too imprecise to definitely document a splitting speciation event; however, the evidence available is consistent with such an interpretation. Morphological variability increases through these sections. Near the top of each stratigraphic range there are two distinct size shifts, first increase in size and then an abrupt decrease in size, after periods of relative stasis in each sample. This may represent a splitting of the more gracile, smaller forms from the larger, more robust forms, either

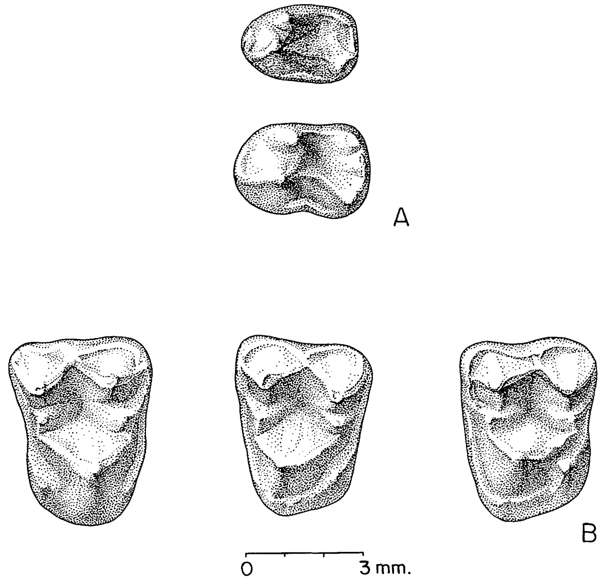

Figure 38. Morphologic changes in lower P_4 and upper molar structure documented in YPM sample of *Microsyops latidens*. A, P_4 changes. In the top specimen (YPM 23136) the oblique cristid is oriented anterior-posteriorly and the talonid is not transversely expanded. In the bottom specimen (YPM 27926) the talonid is transversely expanded and the oblique cristid is more angled. B, molar progression from left to right (YPM numbers 18704, 27807, 23160). Note progressive development of stronger mesostyle, stronger basal cingula, stronger hypocone, and overall robustness.

under conditions of allopatry, or perhaps more likely, under peripatry. This hypothesis is supported by the existence, in later stratigraphic horizons, of two overlapping yet distinct ranges of size and morphology, manifest in *M. knightensis* and *M. scottianus*. I believe that *M. latidens* gave rise to these two species by cladogenesis. Further discussion is provided below. Measurements of *M. latidens* are provided in Table 14.

Microsyops knightensis (Gazin, 1952)

Cynodontomys knightensis Gazin, 1952, p. 20, Pl.2, fig. 1; 1962, p. 41, Pl.1, fig. 7; Robinson, 1963, p. 2; McKenna, 1966, p. 14, figs. 4–6.

Cynodontomys knightensis (in part), Robinson, 1966, p. 39, Pl.4, fig. 2.

Microsyops latidens (in part), Szalay, 1969b, p. 258, Pl.34, figs. 4–9, Pl.36, figs. 3–10, Pl.37, figs. 1–7, Pl.40, figs. 1–7.

Holotype.—USNM 19314, left mandible with P_4-M_3 and alveoli for I_1-P_3, from upper Knight beds, LaBarge fauna, Sublette County, Wyoming (for precise locality data see Gazin, 1952, page 20).

Age and Distribution.—Early Eocene, latest Wasatchian, Wasatchian biochronological zone Wa7 (Lost-

Table 14. Summary statistics for *Microsyops latidens* from various localities. Abbreviations as in Table 1. All measurements in mm. Statistics by collection.

Tooth Position	Parameter	N	OR	$\bar{X}$	S	V
YPM *Microsyops latidens*						
P^3	L	3	2.4–2.65	2.52	0.13	5.0
	W	3	2.3–2.50	2.43	0.12	4.8
P^4	L	4	3.05–3.50	3.30	0.19	5.7
	W	4	3.35–3.75	3.50	0.18	5.1
M^1	L	6	3.3–3.75	3.51	0.16	4.5
	W	6	3.7–4.00	3.86	0.13	3.3
M^2	L	9	3.35–3.95	3.64	0.18	4.9
	W	9	3.65–4.35	4.09	0.25	6.0
M^3	L	10	3.25–3.70	3.49	0.13	3.6
	W	10	3.20–3.95	3.59	0.22	6.1
P_3	L	7	2.15–2.75	2.48	0.22	8.9
	W	7	1.45–1.90	1.66	0.16	9.6
P_4	L	29	2.85–3.60	3.32	0.17	5.0
	W	29	1.85–2.60	2.17	0.16	7.2
M_1	L	44	2.65–3.95	3.44	0.24	6.9
	W	44	2.10–2.75	2.45	0.17	6.8
M_2	L	62	3.25–4.05	3.64	0.21	6.0
	W	62	2.35–3.05	2.73	0.16	5.7
M_3	L	32	3.65–4.45	4.14	0.20	4.8
	W	32	2.20–2.75	2.51	0.12	4.8
USGS *Microsyops latidens*						
P^3	L	1		2.4		
	W	1		1.8		
P^4	L	1		3.5		
	W	1		3.8		
M^1	L	3	3.1–3.4	3.20	0.17	5.4
	W	3	3.1–3.8	3.53	0.38	10.7
M^2	L	4	3.2–3.5	3.39	0.13	3.9
	W	4	3.4–4.1	3.8	0.29	7.7
M^3	L	2	2.9–3.0	2.95		
	W	2	3.2–3.4	3.3		
P_3	L	4	2.3–2.6	2.45	0.12	5.0
	W	3	1.5–1.7	1.58	0.10	6.1
P_4	L	24	2.8–3.7	3.13	0.20	6.4
	W	24	1.7–2.2	1.98	0.13	6.7
M_1	L	39	3.0–3.6	3.25	0.16	5.0
	W	39	2.0–2.7	2.27	0.18	8.1
M_2	L	27	3.1–3.7	3.31	0.18	5.3
	W	27	2.1–2.7	2.37	0.17	7.4
M_3	L	14	3.3–3.9	3.60	0.16	4.5
	W	14	2.0–2.4	2.15	0.18	6.2
AMNH *Microsyops latidens*						
P^3	L	1		3.0		
	W	1		3.2		
P^4	L	1		3.5		
	W	1		3.8		
M^1	L	4	3.1–3.5	3.28	0.17	5.2
	W	4	3.8–4.3	4.0	0.24	6.1
M^2	L	2	3.5–3.6	3.55		
	W	2	4.4–4.6	4.50		
M^3	L	1		3.4		
	W	1		4.3		
P_4	L	4	3.2–3.6	3.35	0.19	5.7
	W	4	2.2–2.5	2.40	0.14	5.9

Table 14. (continued)

Tooth Position	Parameter	N	OR	$\bar{X}$	S	V
M_1	L	12	3.2–3.8	3.55	0.19	5.4
	W	12	2.3–2.9	2.61	0.19	7.4
M_2	L	14	3.6–4.5	3.86	0.25	6.5
	W	14	2.6–3.4	2.97	0.23	7.9
M_3	L	8	3.7–4.7	4.11	0.29	6.9
	W	8	2.2–2.6	2.44	0.14	5.8

cabinian, *Lambdotherium* Range-Zone) and early Bridgerian, Bridger chronological zone Br1 (Bridger A or Gardnerbuttean) of southwestern Wyoming and Colorado.

Emended Diagnosis.—Microsyops knightensis differs from *M. scottianus* by being smaller with less bulbous cusps and a narrower P_4, with hypoconulid centered on the posterior aspect of the talonid (instead of appressed to the entoconid as in *M. scottianus*). Differs from *M. latidens* by having a slightly more progressive P_4.

Discussion.—Gazin described *Microsyops knightensis* from the LaBarge-Big Piney Wasatchian of southwestern Wyoming. He noted that it was similar in size to *M. latidens*, but much smaller than *M. scottianus* with which it was likely to be contemporaneous. *M. knightensis* differed from *M. latidens* by having a more progressive P_4.

Szalay (1969b) synonymized *M. knightensis* and *M. latidens*, but noted that the *M. knightensis* sample was probably Lostcabinian (Wa7), not Lysitean (Wa6) in age, as was *M. latidens*. He felt that the morphological differences were insufficient to warrant specific separation.

The advantage of a stratigraphic framework upon which to array fossil specimens becomes obvious here. The trends discussed above in *M. latidens* towards *M. knightensis* and *M. scottianus* are obscured if the *M. latidens* sample is regarded as one single group with no relative time element added to size and morphology. With stratigraphic ordering, it becomes apparent that *M. latidens* was differentiating into the two later species, and supports Gazin's original hypothesis that *M. knightensis* is distinct from *M. latidens*.

In addition, recent work by Stucky (1984a, 1984b, also see Chapter II) has provided a biostratigraphic zonation for late Wasatchian and early Bridgerian faunas from Wyoming and Colorado. Based on this zonation, the samples of *M. knightensis* are clearly later in time than those of *M. latidens* and provide additional support for the recognition of *M. knightensis* as a distinct species.

Microsyops knightensis could still be viewed as conspecific with *M. latidens* if the evidence for cladogenesis is not accepted. In this case, *M. scottianus* would be viewed as arising gradually from the *M. latidens* lineage. However, the evidence for two morphological and size trends developing within the *M. latidens* sample suggests that character displacement is occurring within this species. Since there is no good evidence of allopatry, perhaps a peripatric speciation event is more likely with isolation of gene pools occurring by ecological and/or behavioral factors not involving direct, physical isolation. This isolation of gene pools results in the development of two new species by cladogenesis, *M. knightensis* and *M. scottianus*. Further sampling of the appropriate stratigraphic intervals should provide additional evidence to support or reject this hypothesis. Measurements of *M. knightensis* are provided in Table 15.

Table 15. Summary statistics for *Microsyops knightensis* from various localities. Abbreviations as in Table 1. All measurements in mm. Statistics by collection.

Tooth Position	Parameter	N	OR	$\bar{X}$	S	V
USNM *Microsyops knightensis*						
P^4	L	4	3.2–3.7	3.38	0.22	6.5
	W	4	3.6–4.3	4.00	0.29	7.3
M^1	L	4	3.4–3.5	3.45	0.05	1.7
	W	4	3.9–4.4	4.18	0.22	5.3
M^2	L	4	3.5–4.0	3.75	0.21	5.6
	W	4	4.5–4.7	4.58	0.10	2.1
M^3	L	4	3.2–3.6	3.38	0.17	5.1
	W	4	3.6–4.0	3.88	0.19	4.9
P_3	L	3	2.3–3.1	2.73	0.40	14.8
	W	3	1.7–2.1	1.87	0.21	11.1
P_4	L	7	3.1–3.8	3.39	0.22	6.5
	W	7	2.1–3.1	2.47	0.33	13.2
M_1	L	19	3.2–4.0	3.52	0.18	5.2
	W	19	2.4–3.2	2.69	0.25	9.2
M_2	L	16	3.4–4.1	3.75	0.19	5.1
	W	16	2.9–3.5	3.02	0.21	6.9
M_3	L	5	3.9–4.3	4.14	0.18	4.4
	W	5	2.6–2.8	2.68	0.08	3.1
AMNH *Microsyops knightensis*						
P_3	L	1		3.2		
	W	1		1.8		
P_4	L	5	3.4–3.8	3.54	0.15	4.3
	W	5	2.5–2.8	2.62	0.11	4.2
M_1	L	6	3.1–3.8	3.63	0.27	7.3
	W	6	2.5–3.1	2.75	0.22	7.9
M_2	L	7	3.5–4.1	3.80	0.21	5.7
	W	7	2.9–3.1	3.00	0.06	1.9
M_3	L	6	3.9–4.5	4.22	0.22	5.3
	W	6	2.7–3.0	2.80	0.11	3.9
U. Colorado *Microsyops knightensis*						
P^4	L	1		3.5		
	W	1		3.8		
M^1	L	1		3.6		
	W	1		4.2		
P_4	L	3	3.3–3.6	3.43	0.15	4.5
	W	3	2.2–2.6	2.40	0.20	8.3
M_1	L	4	3.3–3.8	3.55	0.21	5.9
	W	4	2.5–3.1	2.75	0.27	9.6
M_2	L	1		3.8		
	W	1		3.0		

Microsyops scottianus Cope, 1881

Microsyops scottianus Cope, 1881, p. 188; 1884, p. 217, Pl.24a, figs.26–26a; Szalay, 1969b, p. 262, Pl.38, fig. 1-8, Pl.39, figs. 1–4, Pl.44, figs. 1–7; Osborn, 1902, p. 209, fig. 36; Bown, 1982, p. 63A.

Cynodontomys scottianus, Matthew, 1915, p. 471, fig. 41–43; Robinson, 1966, p. 39, Pl.4, fig. 1.

Cynodontomys ? *scottianus*, Robinson, 1966, p. 39.

Holotype.—AMNH 4748, left mandible with P_4 and part of M_2, and alveoli for other teeth, collected by Jacob Wortman in 1880 from the Lost Cabin beds, Wind River Basin, Wyoming.

Age and Distribution.—Early Eocene, Wasatchian (Wasatchian biochronological zone Wa7, Lostcabinian, *Lambdotherium* Range-Zone) from the Bighorn and Wind River Basins of Wyoming and from Huerfano Park, Colorado. *M. scottianus* may also be present in the early Bridgerian, Bridger zone Br1 (see below).

Emended Diagnosis.—*Microsyops scottianus* differs from contemporaneous *Microsyops knightensis* by being significantly larger.

Discussion.—*Microsyops scottianus* is one of the more enigmatic species of *Microsyops*. It can be distinguished from *M. knightensis* easily based on size and robusticity, but is similar to later *Microsyops* species, particularly *M. elegans*, in size. *M. elegans* differs only in being slightly less robust and in having a slightly more progressive lower third premolar. In addition, *M. elegans* has slightly more dilambdodont upper molars than *M. scottianus*, similar to, but not as developed as those seen in *Craseops* (also apparent in *M. annectens*).

The samples of *M. scottianus* from the Wasatchian are distinctive, but those samples from later horizons are difficult to assess. As Szalay (1969b) pointed out, *M. elegans* is only slightly smaller than *M. scottianus* and may well prove to be the same species when samples improve. However, I believe that there is sufficient evidence to maintain a distinction between these two species. *M. elegans* is known from the early Bridgerian, Bridger zone Br2 (Bridger B, *M. elegans* Assemblage-Zone), while *M. scottianus* is known from the late Wasatchian, Wasatchian zone Wa7. In between these two zones are specimens from Bridger zone Br1 (Bridger A, Gardnerbuttean). The work of Stucky (1984a, 1984b) permits many of these samples to be placed in their proper biostratigraphic interval. Two samples are of particular interest and are discussed below. Measurements of *M. scottianus* are provided in Table 16.

Microsyops, cf. *M. scottianus*

Cynodontomys scottianus, Gazin, 1962, p. 41, fig. 8.

Microsyops scottianus, West, 1969a, p. 83; 1969b, p. 188.

Microsyops elegans, McGrew and Sullivan, 1970, p. 79, fig. 12a.

Microsyops, cf. *M. scottianus*, West, 1973, p. 106.

Table 16. Summary statistics for *Microsyops scottianus* from various localities. Abbreviations as in Table 1. All measurements in mm. American Museum of Natural History collection.

Tooth Position	Parameter	N	OR	$\bar{X}$	S	V
AMNH *Microsops scottianus*						
M^1	L	3	4.1–4.4	4.23	0.15	3.6
	W	3	4.9–5.0	4.97	0.06	1.2
M^2	L	1		4.9		
	W	1		5.6		
P_3	L	3	2.8–3.2	3.03	0.21	6.9
	W	3	2.5–3.0	2.70	0.10	4.8
P_4	L	8	3.4–4.0	3.79	0.19	5.0
	W	8	2.5–3.0	2.76	0.17	6.1
M_1	L	20	3.6–4.6	3.98	0.27	6.8
	W	20	2.7–3.3	3.00	0.15	5.0
M_2	L	19	3.4–4.9	4.15	0.29	7.0
	W	19	2.9–3.8	3.28	0.21	6.5
M_3	L	9	4.1–5.0	4.66	0.33	7.0
	W	9	2.8–3.5	3.07	0.23	7.5

Discussion.—The two main samples of this group come from the Huerfano Formation, Colorado, and from the New Fork Tongue of the Wasatch Formation in southwestern Wyoming. The Huerfano Formation is exposed in the south-central portion of Colorado. Robinson (1966) described the geology and the mammalian faunas from the Huerfano Formation, noting the existence of eleven major fossil localities and a number of smaller ones. Robinson (1966) and Stucky (1984a, 1984b) have placed these localities in a biostratigraphic framework which spans the late Wasatchian (Wa6 or Lysitean and Wa7 or Lostcabinian) through early Bridgerian (Bridger biochronological zone Br1 or Bridger A or Gardenerbuttean). In this sequence, Robinson recognized three *Microsyops* species, *M. knightensis* from the Lysitean, Lostcabinian, and Bridger Br1, *M. scottianus* from the Lostcabinian, and *M. lundeliusi* from Br1 (now placed in a new genus, see below). As was noted above I believe that the Lysitean specimens assigned to *M. knightensis* by Robinson probably represent *M. latidens* instead. The Lostcabinian specimens are assigned to *M. knightensis* and *M. scottianus* without much difficulty as well. The difficulty arises in Bridger biochronological zone Br1.

Figure 39 shows a plot of tooth size for the sample of *Microsyops* specimens from Bridger zone Br1 (from AMNH and UC). The grouping of small specimens is distinct and represents *M. knightensis*. However, the grouping of larger specimens is spread out with two medians at 2.9 and 3.2.

Two possible explanations could account for this highly variable larger group. Robinson (1966) has suggested that *M. lundeliusi* may have exhibited sexual dimorphism in body size. It is possible that *M. lundeliusi* was sexually dimorphic; however, no other plesiadapiform exhibits any

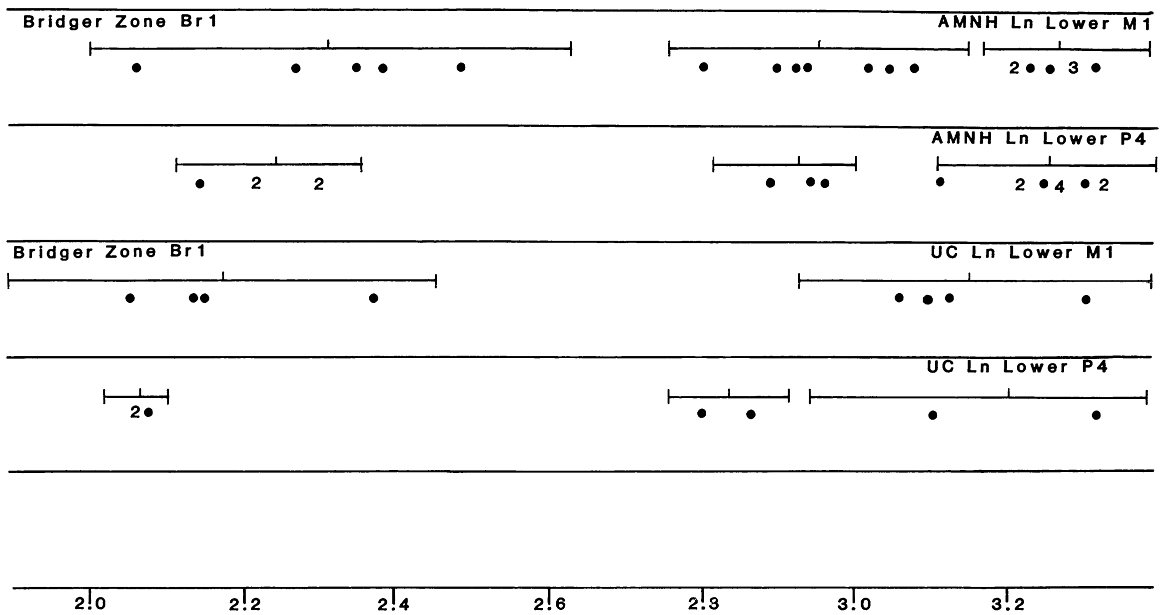

Figure 39. Tooth size plots for AMNH and UC *Microsyops* specimens from Bridger zone Br1. Abscissa represents natural log of tooth area. Solid circles are single specimens, while numbers are multiple specimens of the same tooth dimensions. Horizontal lines bracket two standard deviations on either side of species means (small vertical line).

sign of dimorphism. An alternative explanation of this body size variability lies in the lack of precise stratigraphic positioning for the Huerfano localities and the likelihood of stratigraphic mixing of fossiliferous horizons. None of the Huerfano localities in the early Bridgerian can be placed in stratigraphic superposition relative to each other. This means that some could be older than others within Bridger zone Br1. If the intermediate sized forms were older than definitive *M. lundeliusi* specimens, they would fit into a chronocline from *M. scottianus* to the intermediate form to *M. lundeliusi*. The possibility of sexual dimorphism within *M. lundeliusi* still exists; however, stratigraphic mixing of fossiliferous horizons is a more likely explanation. Until better samples are available, from areas where better stratigraphic control is possible, I choose to place the intermediate sample in *Microsyops*, cf. *M. scottianus*.

Morphologically, this chronocline is also satisfactory, as all of the specimens are robust with bunodont, rounded cusps and less sharply defined crests. The other lineage from *M. knightensis* to *M. elegans* is more gracile, with sharper cusps and crests. The specimens from the New Fork Tongue of the Wasatch Formation referred to *Microsyops*, cf. *M. scottianus*, pose another problem in biostratigraphy. Gazin (1962) originally described the material as *M. scottianus*, noting that it was similar to that species, only slightly larger with a weaker hypocone on the upper molars. West (1969a, 1969b, 1973) further described the geology of the New Fork Tongue and divided it into two lithologic facies, the arkosic facies and the western facies. Gazin's original material came from the western facies (West, 1969a, 1969b). West (1969a, 1969b) also reported *M. scottianus* from the arkosic facies and *M.* cf. *scottianus* from both the arkosic and western facies (West, 1973). Stucky (1984b) examined the mammalian faunas from these two facies and concluded that the western facies was probably Lostcabinian (Wa7) in age, while the arkosic facies may have been younger, perhaps spanning the boundary between the Wasatchian and Bridgerian.

If these specimens all come from the Lostcabinian (Wa7), they probably represent *M. scottianus*. If they are from later in the Lostcabinian and early Bridgerian, they may represent part of the intermediate group between *M. scottianus* and *Megadelphus*. The slightly larger size and the weakening of the hypocone on upper molars are trends suggestive of *Megadelphus lundeliusi*. I have chosen to place these specimens in *Microsyops*, cf. *M. scottianus*, until further information is available for the New Fork Tongue of the Wasatch.

Microsyops elegans (Marsh, 1871)

Limnotherium elegans Marsh, 1871, p. 41.
Microsyops gracilis Leidy, 1872a, p. 20; 1872b, p.363;

1873, p. 83, Pl.6, figs. 14–17; Osborn, 1902, p. 210, figs. 38–39.

Palaeacodon versus, Leidy, 1872b, p. 356.

Bathrodon typus Marsh, 1872, p. 211.

Mesacodon speciosus Marsh, 1872, p. 212.

Microsyops (*Mesacodon*) *speciosus*, Osborn, 1902, p. 212.

Microsyops (*Bathrodon*) *typus*, Osborn, 1902, p. 212.

Microsyops elegans, Szalay, 1969b, p. 269, Pl.39, figs. 7–8, Pl.45, figs. 1–2, Pl.46, figs. 1–8, Pl.47, figs. 1–7; Wortman, 1903, p. 354, figs. 110–111; West, 1973, p. 106.

Holotype.—YPM 11794, left mandible with P_4-M_2, collected from lower Bridger beds, Bridger Basin, Wyoming.

Age and Distribution.—Middle Eocene, Bridgerian, Bridger biochronological zone Br2 (Bridger B, *Microsyops elegans* Assemblage-Zone), from various localities in southwestern Wyoming. Other possible *M. elegans* specimens are known from the Aycross Formation in Hot Springs and Park Counties in Wyoming (see below).

Emended Diagnosis.—*Microsyops elegans* differs from *M. scottianus* by being somewhat smaller, by being more gracile with sharper cusps and crests, and by having better developed hypocones, especially on M^2. *M. elegans* differs from both *M. scottianus* and *M. knightensis* by having more dilambdodont upper molars with very strong, buccally extended mesostyles. It differs from *M. knightensis* by having a strong metaconule on P^4.

Discussion.—*Microsyops elegans* is not very different from *M. knightensis* and these two species could possibly be viewed as conspecific. However, there are a few minor differences, such as the more molariform P^4 and the stronger dilambdodonty, which foreshadow the morphology of *Craseops*. Szalay (1969b) stated that *M. elegans* was known from Bridger A and B (Br1 and Br2), but further refining of these zones suggests that *M. elegans* is restricted to Bridger zone Br2 (Bridger B). *M. elegans* can be viewed as a chronospecies, intermediate between *M. knightensis*, *M. annectens*, and *Craseops*. Another reason for recognizing *M. elegans* as a distinct species comes from the fossil material from the Aycross Formation (see below). This material suggests that *M. elegans* and *M. annectens* may be the result of cladogenesis from *M. knightensis*. Alternatively, *M. annectens* may be viewed as branching off the *M. knightensis*-*M. elegans* lineage.

M. elegans has been described and figured extensively in Szalay (1969b) and nothing of consequence can be added here. Measurements of *Microsyops elegans* are provided in Table 17.

Table 17. Summary statistics for *Microsyops elegans* from various localities. Abbreviations as in Table 1. All measurements in mm. Statistics by collection.

Tooth Position	Parameter	N	OR	$\bar{X}$	S	V
USNM *Microsyops elegans*						
P^3	L	6	2.6–2.9	2.77	0.12	4.4
	W	6	2.9–3.5	3.18	0.22	7.0
P^4	L	8	3.4–3.9	3.63	0.16	4.4
	W	8	4.0–4.4	4.20	0.18	4.2
M^1	L	12	3.5–4.1	3.83	0.20	5.2
	W	12	4.1–5.2	4.47	0.29	6.6
M^2	L	14	3.6–4.2	3.95	0.20	5.0
	W	14	4.5–5.4	4.84	0.33	6.8
M^3	L	9	3.3–4.2	3.67	0.27	7.3
	W	9	3.6–4.8	4.09	0.36	8.8
P_3	L	8	2.5–3.2	2.83	0.22	7.7
	W	8	1.6–1.9	1.80	0.11	5.9
P_4	L	27	3.2–4.2	3.81	0.19	4.9
	W	27	2.5–3.0	2.73	0.15	5.3
M_1	L	30	3.4–4.1	3.76	0.16	4.3
	W	30	2.4–3.0	2.74	0.15	5.3
M_2	L	29	3.5–4.5	3.97	0.23	5.7
	W	29	2.6–3.5	4.10	0.20	6.6
M_3	L	11	4.3–5.0	4.60	0.24	5.2
	W	11	2.8–3.2	2.99	0.14	4.8
AMNH *Microsyops elegans*						
P^3	L	1		2.5		
	W	1		2.7		
P^1	L	1		3.5		
	W	1		3.9		
M^1	L	1		3.3		
	W	1		4.0		
M^2	L	4	3.8–4.2	4.03	0.21	5.1
	W	4	4.7–5.2	5.00	0.24	4.9
M^3	L	3	3.7–4.0	3.87	0.15	3.9
	W	3	4.0–4.5	4.30	0.26	6.2
P_4	L	6	3.4–4.0	3.82	0.24	6.3
	W	6	2.6–2.9	2.73	0.12	4.4
M_1	L	11	3.5–4.1	3.82	0.19	5.1
	W	11	2.5–3.1	2.87	0.17	5.8
M_2	L	14	3.7–4.5	4.13	0.28	6.7
	W	14	2.9–3.6	3.20	0.19	6.0
M_3	L	6	4.2–4.9	4.58	0.26	5.6
	W	6	2.9–3.1	3.07	0.10	3.4

Microsyops, cf. *M. elegans*

Microsyops sp., cf. *M. elegans* (in part), Bown, 1982, p. A47.

Microsyops sp., West, 1973, p. 108, Pl.8, figs. c-d.

Discussion.—The sample of *Microsyops* from the Aycross Formation (see Bown, 1982; Eaton, 1982; Torres, Bartels, and Gingerich, in press) is an enigma for a number of reasons. First, the sample is quite small so that a complete understanding of the morphology and its variation is lacking. Second, the range of sizes exhibited in these specimens is quite large, ranging from *M. elegans*-sized forms to *M. annectens* sized forms. Third, the precise position of the Aycross faunas is not known, but it seems to span the boundary between Bridger zones Br1 and Br2. Fourth, the Aycross Formation is a volcaniclastic facies that outcrops along the flanks of the Absaroka Mountain chain in the central and northern Bighorn Basin. The faunal elements preserved in it are from a much different, upland ecological zone compared to those preserved in the fluvial sediments of the floor of the Bighorn Basin. All of these factors combine to make assessment of these Aycross *Microsyops* specimens difficult.

Stucky (1984b) has reviewed the mammalian faunas from the Aycross horizons and has concluded that they are probably slightly younger than the faunas of the *Paleosyops borealis* Assemblage Zone (Bridger zone Br1 or Bridger A). This would place the Aycross faunas at or slightly above the boundary between Bridger zones Br1 and Br2.

Evidence from the Aycross Formation in Park County supports this interpretation as well. In this area, the Aycross Formation is underlain by the Willwood Formation (see Torres and Gingerich, 1983). *Paleosyops* is found in the uppermost part of the Willwood Formation, indicating that Willwood deposition occurred into the Bridgerian (Torres and Gingerich, 1983). Since the Aycross overlies this, it must be, at least, later Bridger zone Br1 (Bridger A) in age. Eaton (1982) reported Aycross equivalent beds within the Wapiti Formation on Carter Mountain (northwestern Wyoming) which he interprets as Bridger B equivalent, supporting the contention that the Aycross Formation is later than Bridger zone Br1.

The Bridger faunal zones (Bridger zones Br1 through Br3 or Bridger A through Bridger D or E) are not particularly well documented, and faunal biostratigraphic zones have not been well formulated, except for the earliest zone. The Aycross faunas, as they are now understood, appear to be later than earliest Bridgerian, but whether they belong to Bridger zone Br1 or Br2 is not known (nor is it fully known whether there is a faunal distinction between Bridger zones Br1 and Br2). Stucky's (1984b) assertion that the Aycross faunas are later than Bridger A seems to be the best interpretation at this time.

The *Microsyops* specimens from this formation pose a difficult problem. They range in size from typical *M. elegans* and *M. knightensis* to the lower range of *M. annectens*. If the Aycross is viewed as Bridger zone Br1 equivalent, the various specimens could be assigned to *M. knightensis* and *M.* cf. *scottianus*. If they are slightly later in time, they may represent *M. elegans* and the first appearance of *M. annectens*, arising from the *M. elegans* lineage. At the present time it may be best to view these specimens from the latter of the two possibilities. In the transition from *M. knightensis* to *M. elegans*, a well developed metaconule is added to P^4. Some of the Aycross specimens have a metaconule developed, while others lack this cuspule, more like *M. knightensis*. If this is viewed as a transitional sample, a metaconule could be gradually forming through this lineage.

The larger specimens may be representative of the first appearance of *M. annectens*, the result of a branching of the *M. knightensis* lineage at or near the Bridger A-B boundary, with the smaller lineage leading to *M. elegans* and the larger one leading to *M. annectens*. Much further work will be needed to demonstrate or reject this hypothesis.

Additional evidence supporting the position of the Aycross as later than Bridger zone Br1 comes from the Cathedral Bluffs Tongue of the Wasatch Formation in southwestern Wyoming. West (1973) reports the presence of a large species of *Microsyops* from this horizon. Comparisons of his measurements with those of Bown's (1982) measurements for the Aycross sample of *Microsyops* (and my own measurements of these fossils) indicates that West's sample is comparable to the larger specimens from the Aycross sample. The Cathedral Bluffs fauna has been interpreted by Stucky (1984b) as later than the *Paleosyops borealis* zone, or Bridger B (Br2). The presence of a large *Microsyops* species in the Cathedral Bluffs is supportive evidence to interpret the Aycross faunas as Br2 in age.

Microsyops annectens (Marsh, 1872)

Bathrodon annectens Marsh, 1872, p. 211.
Microsyops (*Bathrodon*) *annectens*, Osborn, 1902, p. 213, fig. 40.
Microsyops annectens, Wortman, 1903, p. 360, fig. 116; Szalay, 1969b, p. 270, fig. 20, Pl.39, figs. 9–10, Pl.53, figs. 1–8, Pl.54, figs. 1–7; Eaton, 1982, p. 164, figs. 8A-D.
Microsyops schlosseri Wortman, 1903, p. 361, fig. 117.
Microsyops sp., cf. *M. annectens*, Eaton, 1982, p. 166, figs. 8E, 9A-B.

Holotype.—YPM 11791, left mandible with M_3, from Henry's Fork, Bridger Basin, Wyoming.

Age and Distribution.—Middle Eocene, later Bridgerian, Bridger zone Br3 (Bridger C-E, *Microsyops annectens* Assemblage-Zone), from various localities in Wyoming. Also possibly known from California (see Golz and Lillegraven, 1977).

Diagnosis.—*Microsyops annectens* differs from *M. elegans* by being larger and from *M. kratos* by being smaller.

Discussion.—*Microsyops annectens* is the latest species of *Microsyops* preserved in the Bridgerian Land Mammal Age. Its most striking difference from *M. elegans* is its larger size, although some specimens also possess rugose enamel, which no other *Microsyops* species exhibits. *M. annectens* is known mainly from the later Bridger beds in the Bridger Basin in southwestern Wyoming. Eaton (1982) has recently reported *M. annectens* from the Blue Point Marker horizon on Carter Mountain in northwestern Wyoming. Eaton also reports the presence of some unusually large specimens which he tentatively assigned to *M.* cf. *annectens* from this horizon. I do not believe them to be out of the range of variation expected for *M. annectens* and have included them in that species.

Eaton (1982) also noted the presence of one small tooth from the same horizon (Blue Point Marker beds) which he included in *M.* cf. *elegans*. If this is the case, it provides additional evidence for a cladogenic split from *M. knightensis* into *M. elegans* and *M. annectens*. If both species are present in Bridger zone Br1 (see above) and Bridger zone Br2, then a cladogenic explanation is more suitable than anagenesis from *M. elegans* to *M. annectens*.

Microsyops annectens has been described and figured by Szalay (1969b) and nothing further can be added here. Measurements of various *M. annectens* samples are provided in Table 18.

Table 18. Summary statistics for *Microsyops annectens* from various localities. Abbreviations as in Table 1. All measurements in mm. Statistics by collection.

Tooth Position	Parameter	N	OR	$\bar{X}$	S	V
USNM *Microsyops annectens*						
M^2	L	2	4.8–5.1	4.95		
	W	2	5.9–6.1	6.0		
M^3	L	1		4.9		
	W	1		5.6		
P_3	L	1		3.9		
	W	1		2.1		
P_4	L	4	4.2–4.8	4.55	0.26	5.7
	W	4	3.1–3.2	3.13	0.05	1.6
M_1	L	5	4.4–4.8	4.58	0.18	3.9
	W	5	3.4–4.0	3.64	0.23	6.3
M_2	L	3	4.5–4.9	4.77	0.23	4.8
	W	3	3.7–3.9	3.80	0.10	2.6
M_3	L	2	4.9–5.4	5.15		
	W	2	3.5–3.8	3.65		
AMNH *Microsyops annectens*						
M^2	L	1		3.4		
	W	1		4.5		
P_4	L	2		4.6		
	W	2		3.3		
M_1	L	1		4.7		
	W	1		3.5		
M_2	L	1		5.0		
	W	1		3.9		
M_3	L	3	5.6–6.0	5.8	0.20	3.4
	W	3		3.5		

Microsyops kratos Stock, 1938

Microsyops kratos Stock, 1938, p. 290, Pl. 1, figs. 4–4a; Szalay, 1969b, p. 273, Pl. 55, figs. 1–4.

Holotype.—LACM (CIT) 2232, left mandible with dP_3 (P_3 in crypt), P_4-M_3, and alveoli for I_1 and P_2, found in 1937 from CIT locality 249, in the Friars Formation, San Diego County, California.

Age and Distribution.—The type remains the only specimen of *M. kratos* known. Its age remains enigmatic, although Szalay (1969b) states that it is of early Uintan, middle Eocene in age. Golz and Lillegraven (1977) note that the position of these faunas (from the Mission Valley and Friars Formations) are difficult to correlate with Rocky Mountain faunas, because late Bridgerian and early Uintan faunas from the western interior are poorly known. They note the possibility that the Mission Valley and Friars Formation faunas may be late Bridgerian or early Uintan in age.

Discussion.—*M. kratos* is part of an endemic southern Californian, middle Eocene fauna. Lillegraven (1979) notes that the faunas from this age range share some taxa in common with Rocky Mountain faunas of approximately the same age. Eleven taxa from the Friars and Mission Valley Formations are unique to California, while 19 taxa share some affinities with Rocky Mountain species. In later Californian strata, such as the Sespe and Santiago Formations, the degree of endemism is much higher with 32 uniquely Californian taxa and only 7 taxa shared with Rocky Mountain faunas of approximately equivalent age (middle and upper Uintan, middle Eocene).

This suggests that some degree of faunal interchange was occurring between the Rocky Mountain interior and the California coastal regions during the late Bridgerian and early Uintan, but, by the middle and later Uintan, this faunal interchange was reduced or absent. *M. kratos* remains known only from California but probably was derived from a Bridgerian *Microsyops* species, such as *Microsyops annectens*. Golz and Lillegraven (1977) report the presence of *Microsyops* sp., cf. *M. annectens* from the Mission Valley Formation, which suggests that *M. kratos* may have been derived from a similar species. *M. kratos* has been described and illustrated by Stock (1938) and Szalay (1969b). Measurements of the type specimen are as follows: $dP_3L = 3.8$, $dP_3W = 2.3$; $P_4L = 6.2$, $P_4W = 4.2$; $M_1L = 5.0$, $M_1W = 4.0$; $M_2L = 5.6$, $M_2W = 4.3$; $M_3L = 5.7$, $M_3W = 4.0$; MD = 9.4mm.

Megadelphus, new genus

Cynodontomys, White, 1952, p. 191
Microsyops, Robinson, 1966, p. 41
Microsyops (in part), McKenna, 1966, p. 17; Szalay, 1969b, p. 263

Type Species.—*Megadelphus lundeliusi*

Etymology.—Megas, Gr., large; adelphos, Gr., brother; in reference to the large size of *Megadelphus* and its close relationship with *Microsyops*.

Diagnosis.—I_1 implanted at higher angle to occlusal plane (less procumbent) than *Arctodontomys* or *Microsyops*; I_1 more robust than other genera. I^2 and C^1 reduced, peg-like, not laterally compressed, slicing blades as in *Microsyops* and *Arctodontomys*. I_1 dorsal bulge less robust and blade not as open. C^1 single-rooted.

Discussion.—*Megadelphus lundeliusi* was originally described by White (1952) as a species of *Cynodontomys* (=*Microsyops*). It is from USNM locality 48FR65, south side of Cottonwood (Dry Muddy) Creek, 11 miles NNW of Shoshoni, Fremont County, Wyoming. There is some confusion concerning the age of this locality. *Paleosyops* and *Lambdotherium* are both present (Stucky, 1984a), the only locality where the index fossils of the Lostcabinian (*Lambdotherium*) and early Bridgerian (*Paleosyops*) co-occur. The difficulty is that the precise positions of these specimens from this locality are unknown and it is very possible that they may be from different horizons within the locality. USNM 48FR65 is probably Bridger Zone Br1, although it may be slightly earlier, representing the earliest appearance of *Megadelphus lundeliusi*.

Megadelphus lundeliusi (White, 1952), new combination

Cynodontomys lundeliusi White, 1952, p. 191, fig. 77.
Microsyops lundeliusi, McKenna, 1966, p. 18, figs. 8–10; Robinson, 1966, p. 41, Pl.4, fig. 6; Szalay, 1969b, p. 263, Pl.41, figs. 4–5, Pl.45, figs. 3–4, Pl.48, figs. 1–8, Pl.49, figs. 1–10, Pl.50, figs. 1–5, Pl.51, figs. 1–5, Pl.52, figs. 1–3.

Holotype.—USNM 18371, right mandible with broken M_{1-3}, and parts of left mandible, from the Wind River Basin, Wyoming.

Age and Distribution.—Early middle Eocene, Bridgerian (Bridger biochronological zone Br1) of Wyoming and Colorado.

Diagnosis.—As for genus.

Discussion.—*Megadelphus lundeliusi* has been adequately described and figured by McKenna (1966) and Szalay (1969b). A discussion of its dental adaptations is presented in Chapter VII.

The entire hypodigm of *M. lundeliusi* is known from localities in the Huerfano Basin, Colorado, except for the type specimen. White (1952) described the type locality as late Wasatchian, Lostcabinian (Wa7). However, Stucky (1984a) notes that this locality (48FR76) is in the *Paleosyops borealis* Assemblage Zone (Bridger zone Br1). In that case, *M. lundeliusi* would be restricted to Bridger zone Br1 and would serve as an index fossil for that horizon. Measurements of various samples of *M. lundeliusi* are given in Table 19.

Table 19. Summary statistics for *Megadelphus lundeliusi* from various localities. Abbreviations as in Table 1. All measurements in mm. Statistics by collection.

Tooth Position	Parameter	N	OR	$\bar{X}$	S	V
AMNH *Megadelphus lundeliusi*						
P^3	L	1		4.4		
	W	1		5.2		
P^4	L	1		6.1		
	W	1		7.0		
M^1	L	2	5.8–6.2	6.00		
	W	2	6.7–7.2	6.95		
M^2	L	1		6.3		
	W	1		7.5		
P_3	L	3	4.3–4.6	4.47	0.15	3.4
	W	3	3.1–3.2	3.17	0.06	1.8
P_4	L	11	5.5–6.4	5.88	0.24	4.2
	W	11	3.9–4.8	4.37	0.26	5.9
M_1	L	9	5.4–6.1	5.81	0.26	4.4
	W	9	4.0–4.7	4.42	0.21	4.6
M_2	L	14	5.6–6.7	6.01	0.31	5.2
	W	14	3.9–5.3	4.61	0.31	6.9
M_3	L	6	6.5–7.1	6.72	0.21	3.2
	W	6	3.9–4.7	4.42	0.28	6.3
U. Colorado *Megadelphus lundeliusi*						
P^3	L	1		5.4		
	W	1		5.6		
P^4	L	2	4.5–6.7	5.60		
	W	2	6.1–7.2	6.65		
M^3	L	3	5.4–6.4	5.87	0.50	8.6
	W	3	6.1–7.7	6.70	0.87	13.0
P_3	L	1		4.3		
	W	1		3.5		
P_4	L	2	5.6–6.4	6.00		
	W	2	4.4–4.6	4.50		
M_1	L	4	5.6–6.5	5.98	0.39	6.5
	W	4	4.2–4.6	4.30	0.20	4.7
M_2	L	2	5.4–6.0	5.70		
	W	2	4.5–4.6	4.55		
M_3	L	1		6.7		
	W	1		4.5		

Craseops Stock, 1934

Craseops Stock, 1934, p. 349; Szalay, 1969b, p. 274.

Type Species.—*Craseops sylvestris*.

Included Species.—Type only.

Emended Diagnosis.—Differs from *Microsyops* and *Megadelphus* by having strongly dilambdodont upper molars with a strong mesostyle loph, by lacking metaconules on upper molars, by having the hypoconid positioned well buccally compared to the protoconid on lower molars, by having better developed paracristids with less cuspate paraconids on lower P_4 and molars, and by being less bunodont.

Age and Distribution.—Known from the Sespe Formation, later Uintan (Uintan zone Ui2, Camelid-Canid Appearance-Zone), middle Eocene, of Ventura County, California.

Craseops sylvestris Stock, 1934

Craseops sylvestris Stock, 1934, p. 349, Pl.1, figs. 1–2a; Szalay, 1969b, p. 274, Pl.56, figs. 1–9.

Holotype.—LACM (CIT) 1580, three associated upper molars, M^{1-3}, from the Sespe Formation, CIT locality 180, in Ventura County, California.

Diagnosis.—As for genus.

Description.—Further specimens of *C. sylvestris* allow the description of the following teeth, upper P^3 and P^4, and

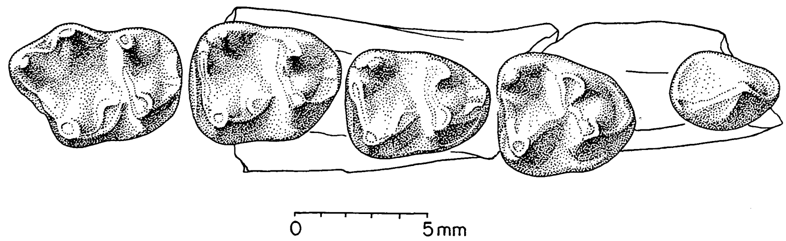

Figure 40. Lower dentition of *Craseops*. Composite right P_3-M_3 (LACM numbers 40222, 40223, 40233), in occlusal view.

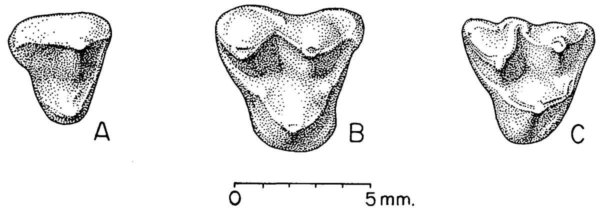

Figure 41. Upper dentition of *Craseops*. A, right P^3 (LACM 40242). B, left P^4 (LACM 40238). C, right dP^4 (LACM 40 237). All in occlusal view.

lower P_{3-4} and M_1, which were previously unknown or undescribed. Figures 40 and 41 show the morphological features described below.

P^3 (LACM 40242) is a three rooted tooth dominated by a tall, sharp paracone. Pre- and postparacristae run anteriorly and posteriorly, respectively, from the apex of the paracone and are sharp and well defined. There is no trace of a metacone. Opposite the paracone and only slightly posterior to it is a sharp, well-developed protocone, much better developed than in any *Microsyops* species. The trigon basin is only slightly developed posteriorly and there are no conules. A weak anterior cingulum joins the preprotocrista.

P^4 (LACM 40238) is more molariform than in any species of *Microsyops* (although approached by *M. elegans* and *M. annectens*). The paracone and metacone are of equal height and are sharply defined. There is a small parastyle, poorly defined, while the parastylar region is slightly inflated, more so than the metastylar region. There is no mesostyle and the stylar shelf is weak. The protocone is lower than the paracone and metacone and less sharply defined. Pre- and postprotocristae diverge widely from the apex of the protocone, forming a broad trigon basin, as in the molars. A weak paraconule is developed on the preprotocrista, but there is no metaconule. There is no hypocone and only a weak posterior cingulum.

P_{3-4} are preserved in LACM 40222, a right mandibular fragment. P_3 is dominated by a tall protoconid. A distinct, strong paracristid is formed along the anterior aspect of the protoconid, running down the anterior flank of the protoconid and curving lingually to the base of the tooth. The paracristid on P_3 is better developed than in any species of *Microsyops*. There is no metaconid. The talonid is low and only weakly formed. There is a small, centrally placed cuspule on the posterior aspect of the talonid, connected to the postvallid by a weak oblique cristid. The talonid extends weakly both buccally and lingually from the oblique cristid, with the lingual half somewhat better developed.

P_4 is quite similar to the molars. There is a strong protoconid and metaconid of equal height, with the metaconid slightly posterior to the protoconid. A very strong, shelf-like paracristid extends from the apex of the protocone to the anterior-lingual base of the metaconid. The hypoconid and entoconid are of equal height and are well developed. The hypoconulid is small and appressed to the entoconid, separated from that cusp by a distinct but shallow notch. The hypoconid is positioned buccal to the protoconid (as in the molars) and is connected to the postvallid by a strong oblique cristid that joins the postvallid centrally. The entocristid is steeply sloping and forms a V-shaped talonid notch. There is a strong buccal cingulid that extends to a weak postcingulid. In comparison with *Microsyops*, the paracristid is much more distinct in *Craseops*, while *Microsyops* often has a more cuspate and lower paraconid.

The first lower molar is preserved in LACM 40223, a right mandibular fragment (also preserving M_2). M_1 is very similar to M_2, which has been described elsewhere (see Stock, 1934; Szalay, 1969b). The protoconid and metaconid are of equal height with the metaconid slightly posterior to the protoconid. The paracristid is as in P_4, but more extended anteriorly, forming a larger shelf. A small paraconid cuspule is present on the anterior aspect of the paracristid. The hypoconid and entoconid are of equal height and well developed. The hypoconulid is small and appressed to the entoconid. As in P_4, the hypoconid is markedly set off buccal to the protoconid (unlike in *Microsyops* in which the hypoconid may be only slightly set off buccal to the protoconid, if at all). There is a strong oblique cristid that joins the postvallid buccal-centrally. A weak mesoconid is developed on the oblique cristid. There is a small buccal cingulid and postcingulid, but they do not join as in P_4.

The entocristid is steeply sloping and forms the posterior portion of a U-shaped talonid notch. Szalay (1969b) felt that a U-shaped talonid notch was characteristic of *Craseops*, but some *Microsyops annectens* specimens also share this feature. Measurements of *Craseops* are provided in Table 20.

Discussion.—*Craseops sylvestris* is part of the Sespe Formation endemic fauna of California. It represents the latest occurrence of a microsyopid known. *C. sylvestris* remains poorly known, and its relationship to other microsyopids remains difficult to define. It is probable that *C. sylvestris* was derived from a *Microsyops* species such as *M. kratos*, but confirmation of this must await further and more complete fossil material.

Table 20. Measurements of *Craseops sylvestris*. Abbreviations as in Table 1. All measurements in mm.

Tooth Position	Parameter	Measurement
P^3	L	3.8
	W	4.1
P^4	L	5.5
	W	5.4
M^1	L	6.1
	W	6.8
M^2	L	6.4
	W	7.0
M^3	L	5.5
	W	5.7
P_3	L	5.3
	W	2.7
P_4	L	5.3
	W	4.4
M_1	L	5.2
	W	4.1
M_2	L	5.6
	W	4.5
M_3	L	6.6
	W	4.5

MICROSYOPINE EVOLUTIONARY PATTERNS-SUMMARY

The University of Michigan Clark's Fork Basin microsyopine sample essentially represents the early radiation of the subfamily (see Figure 42). The measured stratigraphic sections span the latest Paleocene and early Eocene. Microsyopines first appear in the earliest Eocene. *Arctodontomys simplicidens* first appears early in the *Plesiadapis cookei* Lineage-Zone (Cf2) and, as presently understood, is restricted to that zone. Rose (1981) has equated the Paleocene-Eocene boundary with the lithologic change from the drab Fort Union Formation (Paleocene) to the red-banded Willwood Formation in the Clark's Fork Basin. The boundary between Clarkforkian zones Cf1 and Cf2 is near the boundary between the two formations, therefore *A. simplicidens* first occurs in the earliest Eocene. It is known from three localities (UM localities SC-74, SC-137, and SC-143) within Cf2.

Arctodontomys wilsoni first appears in the latest Clarkforkian (Cf3 at UM locality SC-71) and earliest Wasatchian (Wa0 at UM locality SC-67, 10 meters higher stratigraphically than SC-71). It remains a small component of early Wasatchian faunas through Wasatchian zone Wa2, where it abruptly disappears (at Biohorizon A). *Arctodontomys nuptus* appears in Wasatchian zone Wa3 and remains to the end of the biochronological unit.

At the boundary between Wasatchian zones Wa3 and Wa4, *Microsyops* makes its first appearance in the Clark's Fork Basin section, while at the boundary between Wasatchian zones Wa4 and Wa5 (Biohorizon B), *Microsyops cardiorestes* first appears.

Based on first appearance information, *Arctodontomys simplicidens* is an index fossil for Clarkforkian zone Cf2, and also the earliest Eocene. *A. wilsoni* can be used as an index fossil for the early Wasatchian (Wa0), while *A. nuptus* is an indicator of Wa3. *Microsyops angustidens* is an index fossil for Wa4, while *M. cardiorestes* marks Biohorizon B and Wa5.

The fossil record in the Clark's Fork Basin section is lacking in certain ways. *Arctodontomys* is not an abundant taxon so it is difficult to trace the relationships between the three species. *A. simplicidens* probably gave rise to *A. wilsoni*, although by what means (anagenesis or cladogenesis) is unknown. *A. wilsoni* probably led to *A. nuptus*, but again the method of speciation is not suggested by the fossil record. *A. wilsoni* last appears in the Michigan section at the 1750 meter level (Biohorizon A). *A. nuptus* first appears at approximately the 1950 meter level. Gingerich (1985) has estimated that each 10 meter interval in the Clark's Fork Basin represents approximately 27,000 years on average. At this scale, some 500,000 years may be represented between the last appearance of *A. wilsoni* and the first appearance of *A. nuptus*. 500,000 years is more than enough time for *A. wilsoni* to gradually change into *A. nuptus*. However, a punctuational change cannot be ruled out because the record is too poor to test either of these hypotheses.

The interval between the last occurrence of *A. nuptus* and the first appearance of *Microsyops angustidens* is much shorter. Only 45 meters of section separates these two events (see Gunnell, 1985), or about 60,000 years. Two possibilities exist for this evolutionary change. Either a punctuational event is being sampled during this interval, with *A. nuptus* changing rapidly into *M. angustidens*, or the appearance of *M. angustidens* represents a migration into the Clark's Fork Basin.

A similar, but separate, difficulty exists with *M. angustidens* and *M. cardiorestes* (this difficulty is somewhat alleviated in the Yale and USGS sections from the central Bighorn Basin). While in the lower parts of the Clark's Fork Basin section, localities are interspersed throughout the stratigraphic range, near the top of the section, locali-

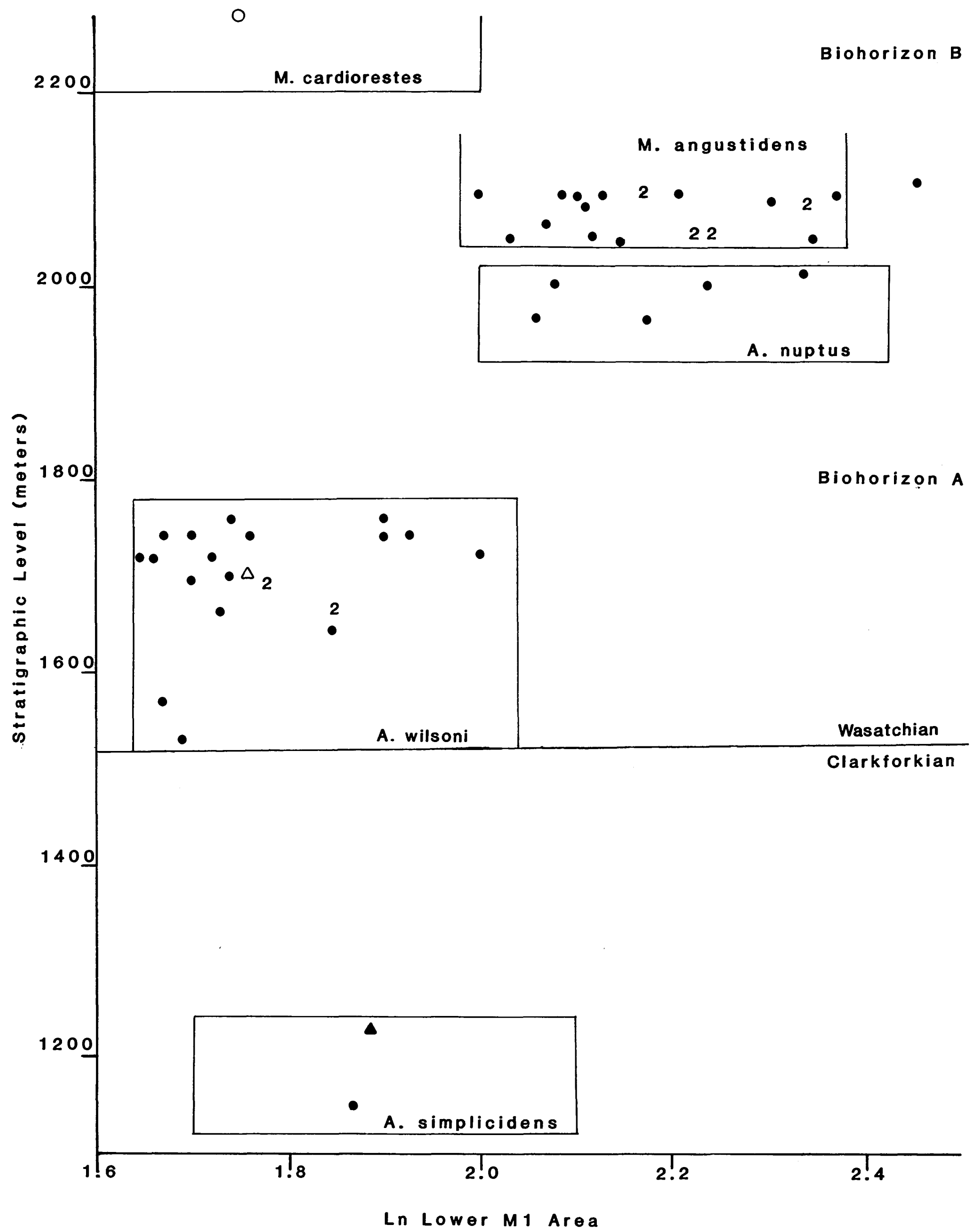

Figure 42. Plot of tooth size and stratigraphic level for UM microsyopine sample. Abscissa represents natural log of lower first molar area. Ordinate represents stratigraphic level in meters. Solid circles represent single specimens, while numbers indicate multiple specimens at the same co-ordinates. Open circle is inferred lower M_1 size for a specimen of *M. cardiorestes* of known stratigraphic position. Solid triangle is holotype of *Arctodontomys simplicidens*, while open triangle is holotype of *Arctodontomys wilsoni* from the central Bighorn Basin (stratigraphic level inferred). Boxes enclose species and approximately two standard deviations on either side of species means for tooth size. See text for further discussion.

ties are far less frequent due to a lack of exposure and more ground cover. The last occurrence of *M. angustidens* is not documented in the Michigan sequence, nor is the last appearance of *M. cardiorestes*. By correlation with other sections (see below), the first appearance of *M. cardiorestes* at Biohorizon B is confirmed. The appearance of *M. cardiorestes* may also represent a punctuation event or a migration event, but the resolution required to answer the question remains unavailable.

The Yale section (see Figure 37) from the central Bighorn Basin, provides further information concerning the later early Eocene radiation of microsyopines and provides confirmation of the general pattern presented by the Clark's Fork Basin section. The pattern in the early part of the section is essentially that of the Michigan section. *Arctodontomys wilsoni* is again present below Biohorizon A (at 200 meters in the Yale section), but not above it. The earliest parts of the Wasatchian (Wa0 and Wa1) are not preserved in the Yale section. *A. nuptus* appears in Wasatchian zone Wa3, but is gone by the end of that biochronological zone.

Microsyops angustidens appears about 100 meters above the last appearance of *A. nuptus*, just below Biohorizon B (at 380 meters) or the boundary between Wa4 and Wa5. Because of the more rapid sedimentation rates in the central Bighorn Basin, this amount of sediment probably represents approximately 500,000 years. Here, three possibilities present themselves. Gradual phyletic evolution between *A. nuptus* and *M. angustidens*, a punctuational event, or immigration all could account for the pattern presented in the Yale section. *M. cardiorestes* appears abruptly at Biohorizon B and may represent either punctuation (from *M. angustidens*) or another immigration event.

The Yale section also preserves microsyopines from later periods in the early Wasatchian. While the Michigan section has no record beyond the beginning of Wasatchian zone Wa5, the Yale section preserves a record through Wasatchian zone Wa6 (above Biohorizon C, the Lysitean subage of the Wasatchian, *Heptodon* Interval-Zone). At Biohorizon C (530 meters in the Yale section), *M. latidens* abruptly appears. *M. latidens* remains common through Wa6 with localities interspersed at approximately 10 meter intervals (approximately 50,000 year intervals).

As *M. latidens* is traced up through the stratigraphic section, the mean size is seen to fluctuate, but to gradually increase, until at the 600 meter level a marked increase in size occurs followed by a rapid size decrease (solid line connects the means from each stratigraphic horizon). As discussed above, I have interpreted this to represent a cladogenic event with the larger sized forms giving rise to *M. scottianus* and the smaller sized forms giving rise to *M. knightensis*. This is not only satisfactory from a size standpoint, but would fit with the two morphological trends within the *M. latidens* sample (see above).

In the Yale section, as in the Clark's Fork Basin section, *Microsyops* species provide useful markers for biochronological zones. The first appearance of *M. cardiorestes* marks the boundary between Wasatchian zones Wa4 and Wa5, or Biohorizon B, while the first appearance of *M. latidens* marks the boundary between Wasatchian zones Wa5 and Wa6 or Biohorizon C. The appearance of these two species abruptly in the fossil record in conjunction with the appearances of a number of other new taxa suggests that these two *Microsyops* species may be part of larger scale immigration events. It is probable, if not likely, that both of these species were derived from *Microsyops angustidens*.

The USGS section (see Figure 34) corroborates much of what is shown in the Michigan and Yale sections, but also adds some information which serves to confuse the picture. The overall picture as demonstrated by the previous two sections is duplicated in the USGS section, with *A. wilsoni* absent above Biohorizon A. There is some confusion as to the exact position of Biohorizon A; Bown, pers. comm., believes that it is around 200 meters, but the *A. wilsoni* sample suggests that it may be earlier, perhaps at 150 meters. *A. nuptus* is present only in Wa3, *M. angustidens* is present in Wa4 and just across Biohorizon B (into Wa5), *M. cardiorestes* abruptly appears at Biohorizon B, and *M. latidens* abruptly appears at Biohorizon C. Within the *M. latidens* sample (although the overall means are slightly smaller), the same general pattern of size increase followed by marked size decrease can be seen as exhibited in the Yale section, but the USGS section preserves another size increase not documented in the Yale sample.

One other important feature is exhibited by the USGS section. At approximately 260 meters, within Wasatchian zone Wa3, there is a smaller microsyopine, contemporaneous with *A. nuptus* (lithosympatric in Stucky's 1984 terminology). I have discussed this sample above and chose to place it in *Microsyops angustidens*. These specimens are morphologically *Microsyops*, not *Arctodontomys*. They are intermediate in size between *M. cardiorestes* and *M. angustidens*, but could be included in either as the small end of the *M. angustidens* range or the large end of the *M. cardiorestes* range. As discussed below, the *Microsyops* sample from the Four Mile area in Colorado also has these two microsyopines (*M. angustidens* and *A. nuptus*). McKenna (1960b) named the small form *"Cynodontomys alfi"* based on the erroneous association of an upper P^4 and M^1 (see above). It may prove to be the case that *"C. alfi"* is a valid species which gave rise to *M. angustidens* and *M. cardiorestes*, but morphologically *"C. alfi"* is similar to both *Microsyops* species. Strictly on stratigraphic evidence, an argument for the validity of *"C. alfi"* could be maintained. Also if *M. cardiorestes* and *M. angustidens* arose through cladogenesis from *"C. alfi,"* by strict interpretation of cladogenesis, *"C. alfi"* would have to be a valid species. However, the evidence for cladogenesis is sparse, particularly because the stratigraphic relationships between the Four Mile samples is unknown, and also because the samples from the USGS section are so meager. I have retained these specimens in *M. angustidens*, thus extending the range of that species into Wasatchian zone Wa3, pending further evidence.

Figures 43 and 44 are compilations of microsyopine specimens housed in the American Museum of Natural History and the United States National Museum, respectively. Figure 45 is a compilation of specimens from the University of Colorado Museum at Boulder. These specimens are from a number of different areas in Wyoming and Colorado, but precise stratigraphic control is often difficult. I have correlated these collections with those of other, more controlled stratigraphic sections, based on the mammalian faunas, exclusive of microsyopids. Using these correlations, I have plotted tooth size against estimated stratigraphic position. I have used the Wasatchian zones and have divided the Bridgerian as described in Chapter II. Although trends within species cannot be studied, the major trends between species can be outlined. It must be kept in mind that each of the samples represents specimens from a number of areas and a number of stratigraphic horizons within each biostratigraphic unit. Table 21 lists the various localities and their assigned position based on my own work and that of Gingerich (1983) and Stucky (1984a, 1984b).

The American Museum sample shows the general size increase present in the Wasatchian, from Wasatchian zone Wa3 (*M. angustidens*), to Wa4-Wa5 (*M. angustidens*) to Wa6 (*M. latidens*) to Wa7 (*M. scottianus*). The *M. scottianus* sample has a larger mean size than *M. scottianus* from the USGS sample (2.48 to 2.22), but the sample from the AMNH represent a lumping of many localities and horizons so that size trends within *M. scottianus* are not reflected. The Wa7 sample from the USNM is superimposed on that of the AMNH sample in Figure 46. The Wa7 sample from the USNM is smaller than that of the AMNH sample and represents the type sample of *M. knightensis*. Although the stratigraphic control is not particularly good, the size ranges of the two samples and the morphological details discussed above justify the recognition of two species and perhaps the cladogenic event mentioned above.

In the latest Wasatchian (Wa7), there is evidence for a splitting of the *Microsyops* lineage into a smaller branch (*M. knightensis*) and a larger branch (*M. scottianus*). By the early Bridgerian (Br1), these two separate lineages are well established. In both the AMNH and UC samples, at least two distinct lineages are present. In both, there is a small lineage representing *M. knightensis*. In the UC sample, there is a single large-sized group representing *Megadelphus lundeliusi*. However, in the AMNH sample, two larger samples appear to be present, one of *M. lundeliusi*, and one intermediate between *M. lundeliusi* and *M. knightensis*. The UC lower first molar plots do not reveal the presence of two larger species, but plots of lower fourth premolars do suggest that two larger sized forms may be present.

Again, because good stratigraphic control is lacking, the status of this intermediate sized group remains unknown. I have placed the fossils in *Microsyops* sp., cf. *M. scottianus*. Robinson (1966) has suggested that these two larger size groups may represent sexual dimorphs of *M. lundeliusi*. Although this is possible, no other *Microsyops* species (or plesiadapiform) shows any sign of sexual dimorphism, and I view this explanation as unlikely, particularly in view of the stratigraphic mixing of horizons within the early Bridgerian.

The AMNH and USNM samples preserve middle Bridgerian (Br2) microsyopines, which are apparently all one species, *Microsyops elegans*. It has been suggested that Bridger A and B samples may not represent markedly different horizons and could be put together. If this is the case, *M. knightensis* and *M. elegans* would be synonymous. Although the size ranges of these two species completely overlap, there are some morphological features (see above) that suggest that the two species are distinct. This also suggests that Bridger A and Bridger B are distinct horizons and that *M. elegans* can be used as an index fossil for Bridgerian zone Br2 (Bridger B).

The later Bridger horizons, Bridger C and D (Bridger zone Br3) are represented in the USNM collections by *Microsyops annectens*. *M. annectens* is similar in morphological detail to *M. elegans* and was likely derived from that species. It is also quite similar to *Craseops* and it is likely that that late Uintan genus was derived from *M. annectens* or a closely similar form (see discussion above).

The final notable area where *Microsyops* fossils are found is the Four Mile area of Colorado. By examining the other mammalian elements of the Four Mile fauna, it may be possible to interpret its position within a biostratigraphic framework based on the Bighorn Basin faunal sequences. There are eight principal localities that contain the representative Four Mile fauna, including: Anthill Quarry, Kent Quarry, East and West Alheit Pockets, Sand Quarry, Despair Quarry, Timberlake Creek, and Timberlake Quarry. Each of these localities is represented by at least 100 specimens (McKenna, 1960b), and many by several hundred specimens. The taxa from these localities used for biostratigraphic determination are those that have been thoroughly studied in the Bighorn Basin. These include *Esthonyx* (Gingerich and Gunnell, 1979), *Cantius* (Gingerich and Simons, 1977), *Labidolemur* (Gingerich and Rose, 1982), *Miacis* (Gingerich, 1983), and three multituberculate genera, *Ectypodus*, *Parectypodus*, and *Neoliotomus* (Krause, 1982).

Table 22 shows the distribution of these taxa from the Four Mile localities. Each of the biostratigraphic zones (Wa1 through Wa3) is based on the first and last appearances of different taxa.

Looking at the faunas from Four Mile, it is apparent that most of the species are indicative of a biostratigraphic position of Wasatchian zone Wa2, based on the first appearance of *Cantius mckennai* and *Ectypodus*, cf. *E. childei*, and the last appearance of *Labidolemur kayi*, *Esthonyx spatularius*,

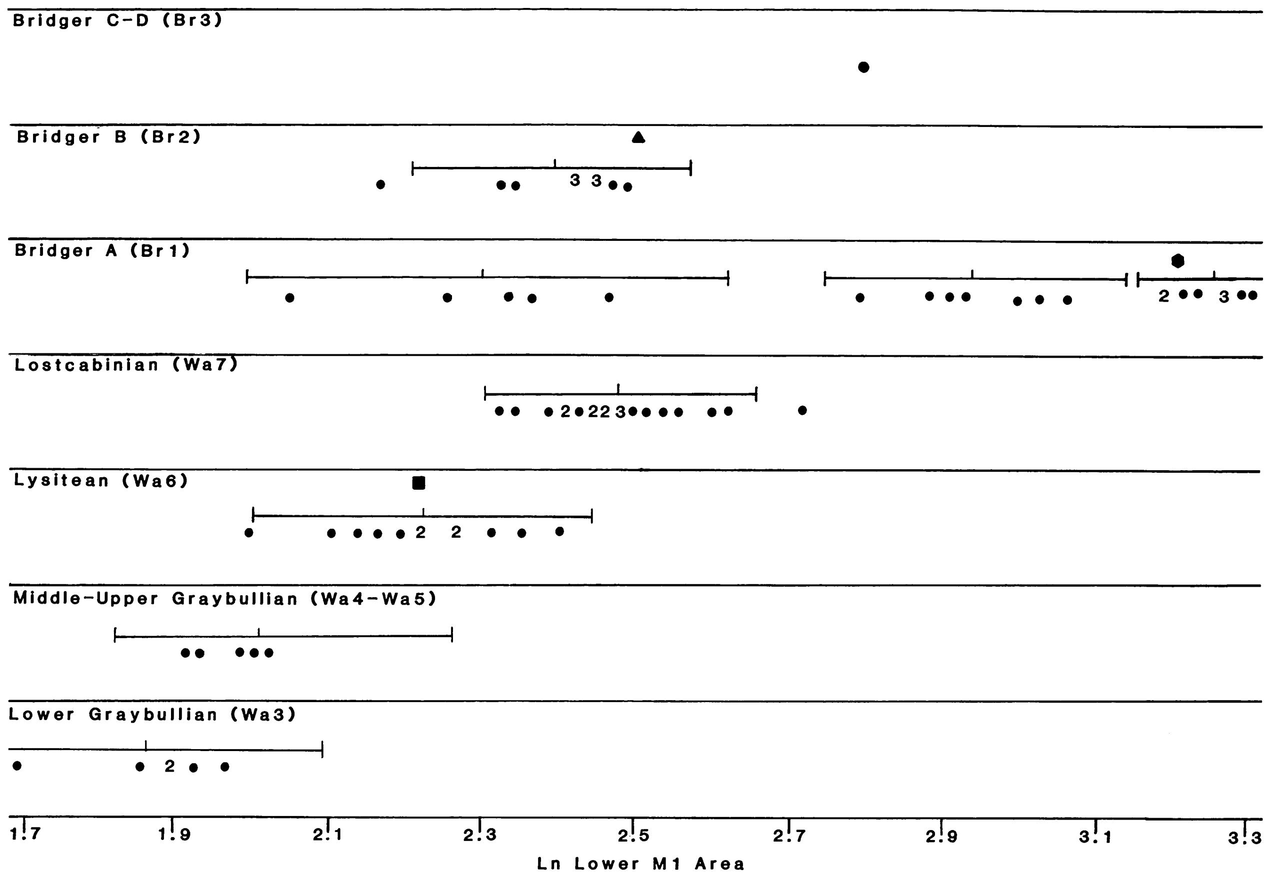

Figure 43. Tooth size plot for AMNH sample of microsyopines. Abscissa represents natural log of lower first molar area. Stratigraphic levels inferred (see text). Solid circles represent single specimens, while numbers represent multiple specimens of the same tooth dimensions. Horizontal bars enclose two standard deviations on either side of species mean (small vertical bar) for each sample. Solid square is holotype of *Microsyops latidens*. Solid hexagon is holotype of *Megadelphus lundeliusi*. Solid triangle is holotype of *Microsyops elegans*. See text for further discussion.

Parectypodus lunatus, and *Neoliotomus ultimus*. However, two species, *Miacis exiguus* (except at Kent Quarry), and *Labidolemur serus* (only at Timberlake Quarry) indicate a slightly younger biostratigraphic age for this fauna. The difficulty with these two genera is that they have not been thoroughly studied from the Four Mile region and their specific allocations are only tentative.

Miacis exiguus (Wa3) is described from the Four Mile fauna. Based on tooth size, the Four Mile specimens fit comfortably within the *M. exiguus* range, documented from the Clark's Fork Basin. Table 23 shows comparative mean measurements for two miacids from the Clark's Fork Basin and the *M. exiguus* sample from Four Mile. Although the Four Mile miacid may represent *M. deutschi*, an indicator of Wa2, the tooth sizes suggest that the Four Mile miacids are more likely to be *M. exiguus* and thus indicative of Wasatchian zone Wa3.

Another indeterminate miacine is also mentioned by McKenna from Sand Quarry and Alheit Pocket. The specimens consists of two upper second molars from Sand Quarry and a single upper second molar from Alheit Pocket. Although these specimens are not described in detail, size ranges are given for these teeth. M^2 measures between 5.0–5.5mm in length for the three teeth and between 7.2–7.8mm in width. These measurements compare favorably with those of *Vassacyon promicrodon* from the Clark's Fork Basin. *V. promicrodon* is also an indicator of Wasatchian zone Wa3 (although there is some recent evidence to suggest that its range may extend to Wa2).

A final species, *Labidolemur serus* may be present at Timberlake Quarry (Gingerich and Rose, 1982). If so, this is also evidence of Wasatchian zone Wa3 mammals in the Four Mile-Sand Wash Basin faunas.

Based on the above discussion, into what biostratigraphic zone does the Four Mile-Sand Wash sample lie? Most of the mammalian fauna indicates Wasatchian zone Wa2 or late Wasatchian zone Wa2, while the possible presence of three other species (*Miacis exiguus*, *Vassacyon promicrodon*, and *Labidolemur serus*) indicate Wasatchian zone Wa3. A separate zonation developed by Schankler (1980)

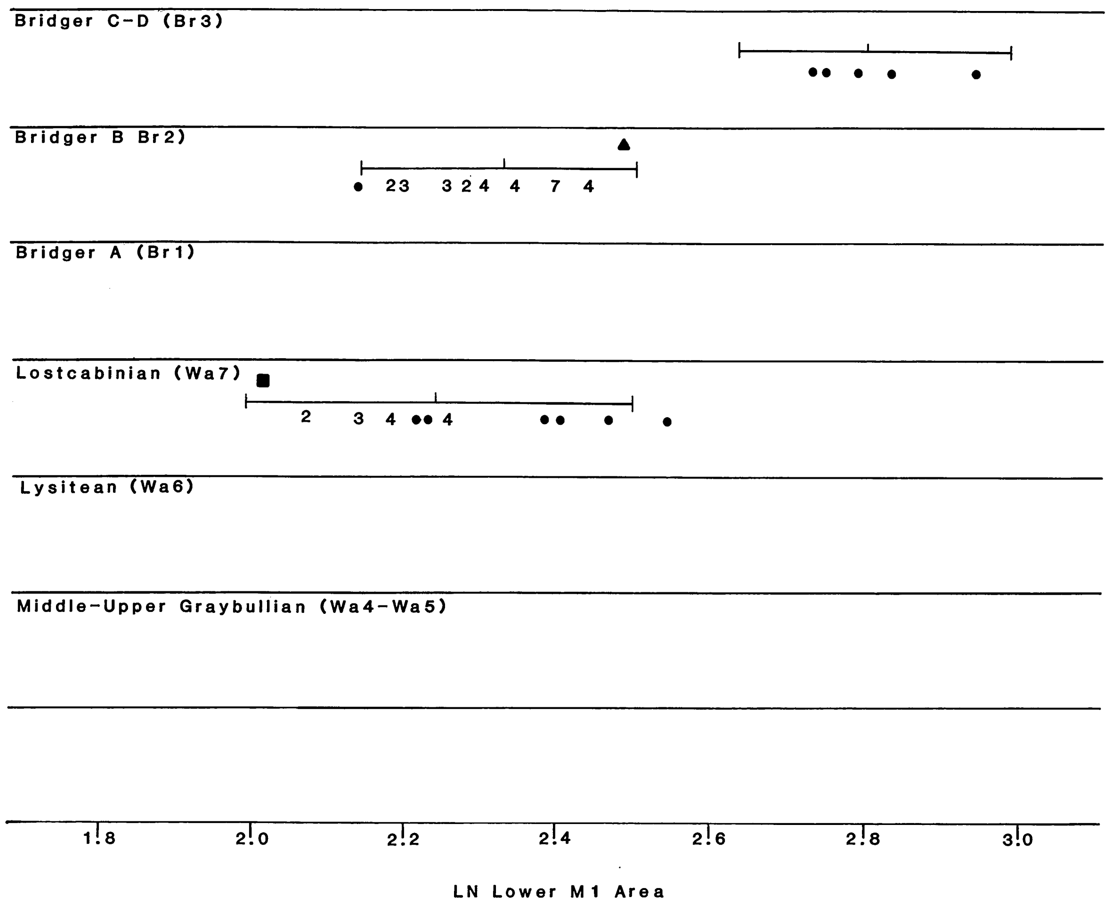

Figure 44. Tooth size plot for USNM sample of microsyopines. Abscissa represents natural log of lower first molar area. Stratigraphic levels inferred (see text). Solid circles represent single specimens, while numbers represent multiple specimens of the same tooth dimensions. Horizontal bars enclose two standard deviations on either side of species mean (small vertical bar) for each sample. Solid triangle is holotype of *Microsyops elegans*. Solid square is holotype of *Microsyops knightensis*. See text for further discussion.

indicates that most of the species discussed above either begin at or span Biohorizon A. Biohorizon A occurs at the boundary between Wasatchian zones Wa2 and Wa3 in the Clark's Fork Basin. I believe, based on the evidence discussed above that the Four Mile mammalian fauna should be placed at or slightly below the Biohorizon A level. This corresponds to a late early Wasatchian age for this fauna.

Szalay (1969b) suggested that East Alheit Pocket may be older than the other Four Mile localities based on the microsyopid specimens. Examination of the other elements of the East Alheit Pocket mammalian fauna does not support this contention, although most of these other taxa remain poorly studied.

The microsyopid fauna is consistent with the biostratigraphic position indicated by the other mammalian faunal elements from the Four Mile localities. Dental evidence suggests that *Arctodontomys wilsoni* is present at East Alheit Pocket, as is *M. angustidens*. This is the first locality in which these two species co-occur and further supports their taxonomic separation, but questions the age of East Alheit. In the Clark's Fork Basin, *A. wilsoni* is present at the Biohorizon A level, while *M. angustidens* does not occur in those sediments. However, in the USGS section, *M. angustidens* occurs just above Biohorizon A, while *A. wilsoni* is present below this horizon. Figure 34 shows a scatter plot of the USGS sample of microsyopines. Biohorizon A is placed at 200 meters, but could be slightly above or below this level. Below this level are specimens which are clearly *Arctodontomys wilsoni*, while above this level are specimens from two distinct species, *A. nuptus* and *M. angustidens*. Comparisons with the Clark's Fork Basin sample shows that the patterns are quite similar, except that *M. angustidens* is not present. Although the diagnostic dental elements for *A. nuptus* are lacking in the USGS

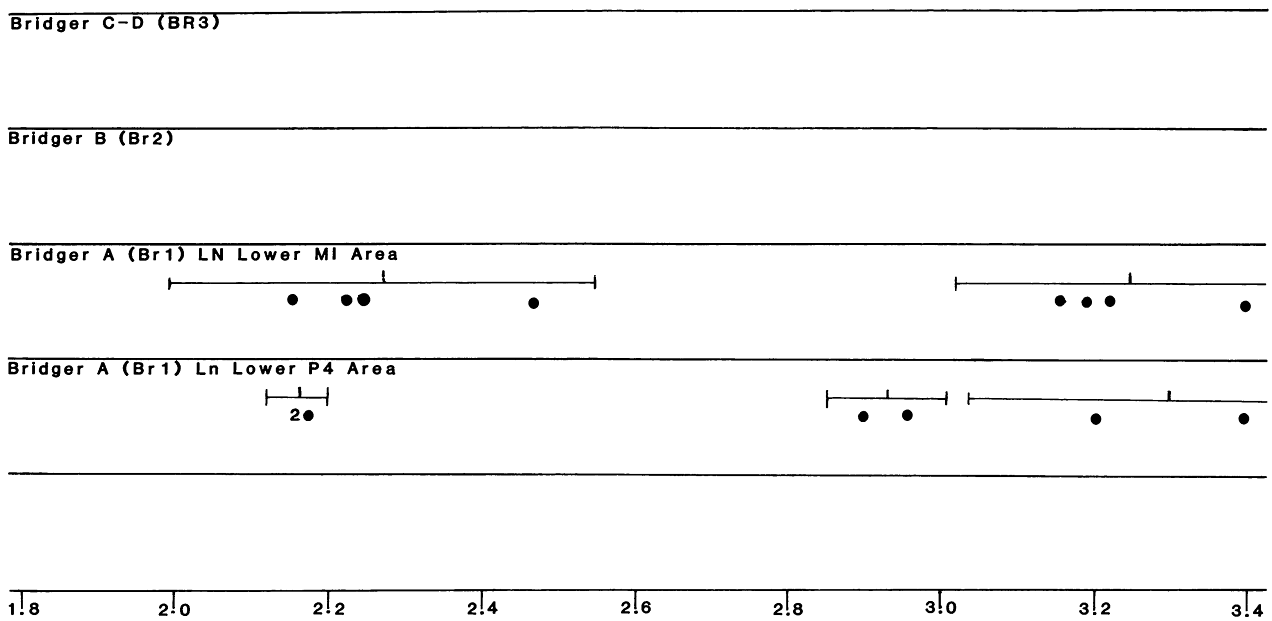

Figure 45. Tooth size plot for UC sample of microsyopines. Abscissa represents natural log of lower first molar area. Stratigraphic levels inferred (see text). Solid circles represent single specimens, while numbers represent multiple specimens of the same tooth dimensions. Horizontal bars enclose two standard deviations on either side of species mean (small vertical bar) for each sample. See text for further discussion.

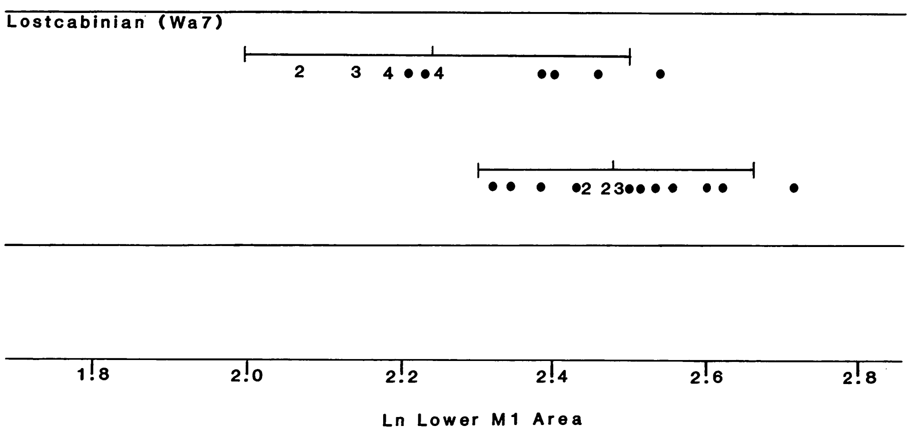

Figure 46. Tooth size plot of AMNH and USNM Wasatchian zone Wa7 microsyopines. Abscissa represents natural log of first lower molar area. Solid circles represent single specimens, while numbers represent multiple specimens of the same tooth dimensions. Horizontal bars enclose two standard deviations on either side of species mean (small vertical bar) for each sample. See text for further discussion.

sample, the tooth size is consistent with *A. nuptus* specimens from the Clark's Fork Basin.

Looking at the tooth size distribution for the Four Mile sample (Figure 47), it is evident that there are three distinct size ranges of microsyopines present. Breaking it down into separate localities, there is clear evidence of two species at Anthill Quarry, East Alheit Pocket, and Alheit Pocket, while at the other localities there is only one species represented. From East Alheit Pocket, as Szalay (1969b) pointed out, there is the small *Arctodontomys wilsoni*, and also the slightly larger *Microsyops angustidens*. The presence of *M. angustidens* at East Alheit

Table 21. Assigned stratigraphic position for various Eocene localities, Wasatchian biochronological zones Wa2–Wa7 through Bridgerian biochronological zones Br1–Br3.

Wa2–Wa3	Wa4–Wa5	Wa6	Wa7	Br1	Br2	Br3
Sandcouleean	Middle Graybull	S. Elk Creek	Wind River Basin	Upper Huerfano	Bridger B	Bridger C
Powder River 51–42	Upper Graybull	Cottonwood Draw	Lost Cabin	Huerfano II	East Grizzly Butte	Bridger D
East Alheit Pocket	*Coryphodon* Beds	Huerfano VIII	Alkali Creek	Fossil Creek	W. Grizzly Butte	Bridger D_1
Powder River 51–62		Knight Fm.	Wind River Fm.	Huerfano Basin	Grizzly Buttes	Bridger D_5
Powder River 51–24		15 Mi. Creek	Alkali Creek LC	Huerfano I	Bridger B_3	Bridger D_2
Powder River 53–3	S. Bitter Creek Station	Bad Water/Poisson	3 Mi. N. Gardener			
Powder River 51–45		Lysite	Creeks Divide LC	Huerfano III		
Sand Wash Basin		15 Mile Creek Lysite	Huerfano Apadock Gulch	Muddy Divide		
Sand Quarry		5 Mi. Creek Lysite	Dry Muddy Creek	NW of Gardener		
Powder River 51–44		Lysite Wind River	Huerfano VI	Huerfano V		
Powder River 51–22			LaBarge	AMNH Loc. II		
Powder River 51–21			Muddy Creek	Sullivan Ranch (Anthill)		
Powder River 51–13			East Green River			
Powder River 41–33			N. of Big Piney	Bridger A		
Powder River 51–60			S.Green/New Forks River Junction			
Powder River 52–26			Knight-New Fork Member			
Powder River 51–59			Fogarty Draw			
Powder River 51–10			Huerfano IV			
Powder River 51–17						
Powder River 51–7						
Powder River 52–27						
Despair Quarry						

Pocket suggests that this locality is not older than the other localities in the Four Mile area, a point supported by the other mammalian faunal elements. At Anthill Quarry, the dominant microsyopine is *M. angustidens*, but there is also one specimen of a larger form (see Figure 47), representing *A. nuptus*. Here, as in the USGS sample, the diagnostic dental elements are lacking, but the tooth size is compatible with *A. nuptus* from the Clark's Fork Basin. In the other Four Mile localities, the only microsyopine is *M. angustidens*.

Summarizing the Four Mile microsyopines leads to the following conclusions. The faunal analysis indicates a biochronological age which corresponds to the boundary between Wasatchian zones Wa2 and Wa3 (Biohorizon A). This indicates a late early Wasatchian age for these microsyopines.

The presence of three distinct microsyopine taxa in the Four Mile fauna is of great interest because it is one of the few places where more than one taxon co-occurs. Two possible explanations for the sudden appearance of the *Microsyops* lineage in the Clark's Fork Basin were postulated above. The available evidence can be interpreted as a punctuational event, with *Arctodontomys* giving rise to *Microsyops* in the late early Wasatchian, or it can be interpreted as an immigrational event, with *Microsyops* entering the basin from an outside area and rapidly replacing *Arctodontomys* in the early Wasatchian. The paleontological evidence may never be complete enough to solve this question. However, there are some pieces of evidence which may favor a migrational interpretation.

At the end of the Paleocene and into the Eocene the climate in the North American interior grew warmer (see Chapter III) with local climates becoming more tropical and less temperate and seasonal. These climatic changes correspond with the appearance of a number of typical Eocene orders such as perissodactyls, artiodactyls, and primates of modern aspect (adapids and omomyids). Most of the Eocene taxa probably immigrated from Europe across the North Atlantic or from Asia across the Bering Straits. The older tropical families which persist into the Eocene, including microsyopids, were probably restricted to a more southern distribution during the cooler, dryer Paleocene

Table 22. Summary of biochronologically relevant Four Mile taxa (* indicates taxon restricted to zone). Taxa listed by locality. Wa1–Wa3 are Wasatchian Land-Mammal Age biochronological zones.

Locality	Wa1-Wa2	Wa3
Anthill Quarry	*Esthonyx spatularius* *Phenacodus primaevus* *Phenacodus intermedius* *Haplomylus speirianus* **Hyopsodus loomisi* **Cantius mckennai*	*Esthonyx spatularius* **Miacis exiguus* *Phenacodus intermedius* *Phenacodus primaevus* *Haplomylus speirianus* **Hyopsodus miticulus*
Kent Quarry	*Labidolemur kayi* *Niptomomys doreenae* *Esthonyx spatularius* **Cantius mckennai*	**Ectypodus* cf. *E. childei* *Labidolemur kayi* *Niptomomys doreenae* *Esthonyx spatularius* **Miacis exiguus* **Hyopsodus miticulus*
Despair Quarry	*Labidolemur kayi* *Niptomomys doreenae* *Esthonyx spatularius* *Pachyaena ossifraga* *Phenacodus primaevus* *Haplomylus speirianus* **Hyopsodus loomisi* **Cantius mckennai*	**Ectypodus* cf. *E. childei* *Labidolemur kayi* *Niptomomys doreenae* *Esthonyx spatularius* Pachyaena ossifraga **Miacis exiguus* *Phenacodus primaevus* *Haplomylus speirianus* **Hyopsodus miticulus*
W. Alheit Pocket	*Ectypodus tardus* *Neoliotomus ultimus* *Labidolemur kayi* **Cantius mckennai* *Phenacodus intermedius* *Ectocion osbornianus* *Haplomylus speirianus* **Hyopsodus loomisi* *Parectypodus lunatus* *Tetonius mckennai*	*Ectypodus tardus* *Neoliotomus ultimus* *Labidolemur kayi* **Miacis exiguus* *Phenacodus intermedius* *Ectocion osbornianus* *Haplomylus speirianus* **Hyopsodus miticulus* *Parectypodus lunatus*
E. Alheit Pocket	*Ectypodus tardus* *Parectypodus lunatus* *Neoliotomus ultimus* *Labidolemur kayi* **Cantius mckennai* *Esthonyx spatularius* *Pachyaena ossifraga* *Haplomylus speirianus* **Hyopsodus loomisi* *Tetonius mckennai*	*Ectypodus tardus* *Parectypodus lunatus* *Neoliotomus ultimus* *Labidolemur kayi* *Esthonyx spatularius* *Pachyaena ossifraga* *Haplomylus speirianus* **Hyopsodus miticulus* **Miacis exiguus*
Sand Quarry	*Ectypodus tardus* *Parectypodus lunatus* *Neoliotomus ultimus* *Labidolemur kayi* **Cantius mckennai* *Esthonyx spatularius* *Haplomylus speirianus* **Hyopsodus loomisi*	*Ectypodus tardus* *Parectypodus lunatus* *Neoliotomus ultimus* *Labidolemur kayi* *Esthonyx spatularius* **Miacis exiguus* *Haplomylus speirianus* **Hyopsodus miticulus*

Table 22. (continued)

Locality	Wa1-Wa2	Wa3
Timberlake Creek	**Cantius mckennai*	*Haplomylus speirianus*
	Haplomylus speirianus	**Hyopsodus miticulus*
Timberlake Quarry	*Ectypodus tardus*	*Parectypodus lunatus*
	Parectypodus lunatus	*Neoliotomus ultimus*
	Neoliotomus ultimus	*Labidolemur kayi*
	Labidolemur kayi	**Labidolemur serus*
	**Cantius mckennai*	*Esthonyx spatularius*
	Esthonyx spatularius	**Miacis exiguus*
	Phenacodus primaevus	*Phenacodus primaevus*
	Phenacodus intermedius	*Phenacodus intermedius*
	Ectocion osbornianus	*Ectocion osbornianus*
	Haplomylus speirianus	*Haplomylus speirianus*
	**Hyopsodus loomisi*	**Hyopsodus miticulus*
	Ectypodus tardus	

Table 23. Measurements of *Miacis exiguus* and *Miacis deutschi*. Abbreviations as in Table 1. All measurements in mm. Statistics by geographic area (measurements from McKenna, 1960 and Gingerich, 1983).

Tooth Position	Parameter	Measurement
Clark's Fork Basin *M. exiguus*		
M_1	L	5.45
	W	3.76
M_2	L	4.13
	W	3.09
M^2	L	5.00
	W	7.30
Four Mile *M. exiguus*		
M_1	L	5.40
	W	3.50
M_2	L	3.90
M^2	L	4.30
	W	6.80
Clark's Fork Basin *M. deutschi*		
M_1	L	4.92
	W	3.28
M_2	L	3.80
	W	2.78

and began to spread northward in the subsequent warming period at the beginning of the Eocene.

The Four Mile localities represent the most southern of the northern interior faunas that contain a significant number of microsyopines. These localities provide evidence that suggest that a *Microsyops* migration entering from the south may have led to the extinction of *Arctodontomys* and its replacement by *Microsyops*. While this conclusion is certainly no more than tentative, the pattern presented is consistent with a migrational interpretation but further evidence is needed to support or reject this hypothesis.

The Eocene record of *Microsyops* and *Arctodontomys* provides much evidence concerning the patterns of species level evolution and the relationships between species. Another aspect of the abundance of Eocene microsyopine fossils is that they provide an opportunity to study the paleobiological aspects of these genera, particularly by close examination of dental functions. The following chapter examines dental function in microsyopines, as well as dental function in early taxa such as mixodectids and palaechthonids.

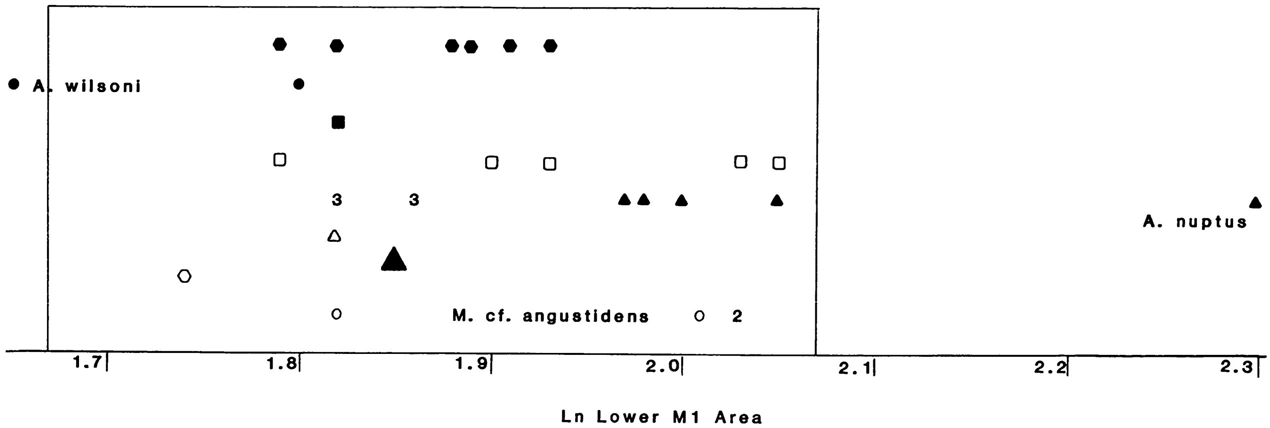

Figure 47. Plot of tooth size of microsyopines from Four Mile Fauna sample. Abscissa represents natural log of first lower molar area. Solid hexagons represent specimens from Despair Quarry, solid circles are East Alheit Pocket, solid squares are Timberlake Creek, open squares are Sand Quarry, solid triangles are Anthill Quarry, open triangle is Kent Quarry, open hexagon is West Alheit Pocket, and open circles are Timberlake Quarry. Large solid triangle represents the mean for *Microsyops*, cf. *M. angustidens*. Numerals represent multiple specimens of the same tooth dimensions from a given locality. See text for further discussion.

VII
DENTAL FUNCTION OF MICROSYOPOIDEA

In the previous four chapters, I have reviewed the evolutionary history and relationships of the microsyopoid families Palaechthonidae and Microsyopidae, as well as the relationships of Mixodectidae. In this chapter, I concentrate on the structure of the dentitions in these groups, not from a taxonomic viewpoint, but from a functional point of view. Incisor function in palaechthonids and microsyopids is discussed first and then the attributes of the molar dentitions in these groups and mixodectids is reviewed. Quantification of relative shearing and crushing surfaces is presented for certain taxa of plesiadapiforms and primates.

First the relationships between tooth size and body size are reviewed. A discussion of body size and its influence on dietary reconstruction follows. In a final section, I discuss tooth function and its relationship to the plesiadapiform-primate dichotomy.

Incisor Form and Function

The most distinctive characteristic of plesiadapiforms is the presence of a pair of enlarged, procumbent lower incisors. These incisors differ in form (and presumably function) among the various families, but are, for the most part, generally similar. Within plesiadapiforms, some taxa possess more than one pair of lower incisors but in no taxon (except perhaps *Purgatorius*) in which incisor morphology is well known do lower lateral incisors participate in the same functional role as the lower central incisors. Some plesiadapiform taxa emphasize the role of their incisors more than others (for example, *Chiromyoides* possesses a very large incisor and reduced cheek teeth), but in all taxa, the lower central incisor figures prominently in the food processing mechanism.

The lower incisor of microsyopoids has a peculiar lanceolate shape. From the base, the ventral border extends anteriorly and gently curves dorsally to the tip. The dorsal border bulges outward then curls ventrally to the tip. The blade is dish-shaped or leaf-shaped posteriorly and forms a tapered point anteriorly. The entire blade curves somewhat lingually from base to tip.

On this general morphological pattern there is a great deal of variation among the various taxa included in microsyopoids. In *Microsyops*, the blade of I_1 is oriented dorsal-ventrally and opens slightly buccally. In Paleocene genera, such as *Plesiolestes* and *Palenochtha* the incisor is of a differing form. In both genera, the dorsal bulge distinctive of *Microsyops* is less well developed. In *Plesiolestes*, the blade is open buccally, while in *Palenochtha*, the blade is oriented much as in *Microsyops*. In the later Paleocene microsyopid, *Navajovius*, the dorsal bulge is better developed than in *Plesiolestes* or *Palenochtha*, but the blade is opened somewhat buccally as in *Plesiolestes*. In the Eocene diminutive microsyopid *Niptomomys*, the blade has a dorsal bulge as developed as in *Navajovius* (not as well developed as in *Microsyops*), but the blade is oriented much more dorsal-ventrally as in *Microsyops*.

Within Eocene Microsyopids, two patterns occur, one for all *Microsyops* species, and another for *Megadelphus lundeliusi*. In *Microsyops* I_1 is implanted at a rather low angle (20 to 25 degrees) relative to the occlusal plane. The incisor is extended far forward and the tip of the incisor is at the same level as the occlusal plane (or slightly above it). The blade is oriented dorsal-ventrally and is opened buccally. The dorsal-posterior bulging of the incisor blade is most prominent in *Microsyops*.

I examined the wear striations on microsyopoid incisors using a light microscope and mounting small pins on the teeth in the orientation of the wear striations present. Examining the wear striations of *Microsyops* reveals the following pattern. First, wear caused by the two incisors rubbing against one another is confined to the anterior third of the teeth, indicating that these incisors only came together near the tips and that some amount of space was present between the posterior two-thirds of these teeth. The wear striations on the interstial facets are oriented dorsal-ventrally and indicate that some degree of independent movement for each mandibular half was possible in a dorsal-ventral direction (the presence of an unfused symphysis supports this suggestion).

The wear striations on the incisor blades themselves are particularly interesting. First, wear striations are present on both the buccal and lingual surfaces of the blade and often extend well down the surfaces of the blade on both sides. The striations are generally oriented dorsal-anteriorly to ventral-posteriorly indicating that they were formed by an upward and forward movement of the mandibles. However, there are some striations which indicate only upward movement of the mandibles, and still others which indicate an upward and backward movement. It appears that the dominant motion was upward and forward. However, other movements were mechanically possible.

The fact that the wear striations extend down both the buccal and lingual surfaces of the blade suggests that most were formed by tooth-food contact, not tooth-tooth contact. The presence of distinct wear striations also supports this, as most tooth-tooth contact produces only a polishing type of wear. The orientation of the incisors and their distinctive wear patterns suggest that these teeth were used as long slicing blades. To achieve a slicing action, the I_1 must have sliced against a similar blade-like morphology in the upper dentition. Figure 48 shows AMNH 55225 (right mandible of *M. knightensis* with I_1, P_4-M_3) occluded with USGS 9194 (right maxilla of *M. latidens* with I^{1-2}?, C^1-M^2). Although these specimens are of different species, the occlusal relationships can be discerned between upper and lower incisors and the upper canine.

The first question to be asked is what is the upper dental formula of *Microsyops latidens*? In my description above, I stated that the upper dental formula was 2–1–3–3. From the occlusal relationships shown here, it is possible that a third incisor was present anterior to the anterior-most incisor preserved in USGS 9194. Gingerich (1976) has suggested that the curious two-cusped, can-opener-like incisors found in Eocene sediments in North America may be *Microsyops* upper central incisors. None have ever been found in place in a dentition, and associations of individual teeth are tentative. Gingerich and Rose (1982) have described the dentition of *Labidolemur kayi*, an apatemyid from the Clarkforkian Land-Mammal Age that has these odd two-cusped incisors. However, many of the incisors found in later Wasatchian deposits appear too large for any known apatemyid and may represent *Microsyops*. Until conclusive evidence is found, the assignment of these incisors to *Microsyops* must remain tentative.

A second possibility for the fact that I_1 extended well past the preserved upper anterior incisor shown in Figure 48 is that USGS 9194 is somewhat crushed at its anterior aspect. The premaxilla has been displaced dorsally and it is possible that it may have been displaced posteriorly, as well. In both *M. elegans* and *Megadelphus lundeliusi*, there are small diastemata between C^1 and I^2 or I^3, while there is no diastema preserved in USGS 9194. However, even if the premaxilla has been displaced posteriorly, it probably has not been moved far, so the possibility of an additional anterior incisor still exists.

In any case it is evident from Figure 48 that if the mandible moved upward and forward, the I_1 would have sliced past the C^1 and I^{1-2}?. All three upper teeth are laterally compressed and as a unit form a long shearing surface along which the I_1 sliced. If mandibular movement is interpreted correctly, in the buccal phase of jaw motion (see below), I_1 would have begun to slice along C^1 and I^2? and proceeded into centric occlusion by slicing past I^{1-2}?. A further point to note is that when the cheek teeth are in occlusion, I_1 is also in occlusion with at least I^1? and probably I^2? as well. *Microsyops* can be characterized as having very procumbent, slicing lower incisors that cut against laterally compressed, blade-like upper canines and incisors. The incisor-canine complex is in occlusion at the same time that the cheek teeth are in occlusion and probably operated as part of the same mechanical system.

Megadelphus lundeliusi is quite different from *Microsyops*. Where *Microsyops* has I_1's implanted at rather low angles to the occulsal plane (20 to 25 degrees), *M. lundeliusi* has its incisors implanted at a much higher angle (45 to 50 degrees). Consequently, I_1 is less procumbent and more projecting in *M. lundeliusi*, projecting well above the occlusal plane. The roots of I_1 are somewhat less laterally compressed in *M. lundeliusi*, and the I_1 is generally much more robust than is typical of *Microsyops*.

Examination of the I_1 wear facets also reveals a number of differences from *Microsyops*. First, wear facets that were limited to the incisor tips in the smaller species extend the full length of the lingual-ventral surfaces of I_1. This suggests that the central incisor pair were in contact down their full length, which I interpret as a sign of stability and strengthening in the incisor region of *M. lundeliusi*. Wear striations along these surfaces show again that some limited dorsal-ventral independent movement was possible for each jaw, but wear striations extending the length of the incisors indicate a more stable symphysial region than was evident in *Microsyops*.

Wear surfaces on the incisor crowns are much different in *M. lundeliusi* as well. There are no wear facets along the buccal and lingual surfaces of the blade of I_1. Wear facets are limited to the anterior-buccal surfaces of the tips of the incisors. Two small confluent wear facets are present on the tips of *M. lundeliusi* incisors. The wear striations indicate that these facets were formed by an upward and slightly forward movement of the mandible.

Gingerich (1974, 1976) has discussed the presence of an orthal retraction (OR) facet on premolars of *Phenacolemur*, *Adapis*, and other mammals. This OR facet is formed by an upward and slightly backward movement of the mandible during the initial phase of the mammalian chewing cycle (for a discussion of primate chewing mechanics and the relationship of these mechanics to wear surfaces see Kay and Hiiemae, 1974a, 1974b; Kay, 1973). During this phase, food is initially broken down by puncturing between the cusps of teeth (see below). I view the incisor wear shown by the teeth of *M. lundeliusi* to be an analogous situation. The incisors of *M. lundeliusi* were not used for slicing, as are those of *Microsyops*, but were used to grasp and initially puncture food items.

Figure 49 (top) shows AMNH 55284 (skull of *M. lundeliusi*) in incisor occlusion with AMNH 55285 (left mandible of *M. lundeliusi* with I_1, P_3-M_3). Two things are apparent from the figure. First, while the incisors are in occlusion, the cheek teeth series are not in contact with one another. The mandible must be shifted forward to bring the upper and lower incisors into contact in such a way to produce the incisor wear striations shown on I_1. The second point is that at no time does I_1 come into contact with either

Figure 48. Occlusal relationships in *Microsyops* species. Note that both incisors and cheek teeth are in occlusion simultaneously. Upper dentition is USGS 9194, lower dentition is AMNH 55225.

I^2 or the upper canine. I^2 and the upper canine are reduced, rather peg-like teeth that are not particularly laterally compressed. The wear patterns on these teeth show a general smoothing and rounding of the tips but no distinct wear patterns.

The upper central incisors of *M. lundeliusi* are robust and pointed. They are much larger than I^2 which is reduced and peg-like. They are not two-cusped and can-opener-like as predicted by Gingerich (1976), but *M. lundeliusi* differs significantly from *Microsyops* and two-cusped upper incisors may still be typical of the latter genus.

The wear patterns on I^1 indicate that I_1 wears against the apex and posterior-lingual portions of the upper incisor. Additional wear on the upper incisor indicates that the anterior surface from the apex dorsally are heavily worn by tooth-food contact. The heaviness of the wear indicates that the diet probably consisted of very abrasive food stuffs (as does wear on the molars, see below).

The function of the lower incisors of *M. lundeliusi* and their morphology differs from that of *Microsyops*. The I_1 of *M. lundeliusi* was used to puncture and grasp food during an initial stage of the chewing cycle, not to slice food as in *Microsyops*. The incisors of *M. lundeliusi* differ in morphology by being more vertically implanted, by having a less well developed dorsal bulge, by being more robust, by projecting well above the plane of the cheek teeth, and by being more dorsal-ventrally aligned and not as open buccally. The two incisors together served as a powerful puncturing and splitting tool used in the initial preparation of food for further mastication. Together they may have functioned as a wedge or "beak" to puncture and break up hard food objects.

Two types of incisor function are indicated within Eocene microsyopids based on the above interpretation: one predominantly slicing, the other puncturing and splitting. The morphological attributes of each incisor type should serve as models to which other taxa within microsyopoids can be compared in order to interpret their incisor functions. Slicing incisors can be characterized as follows: 1) very procumbent with tips not extending much above the plane of the cheek tooth series; 2) incisor blades dorsoventrally aligned but opened somewhat buccally, often with a well developed dorsal bulge which enables further slicing against the upper canine and perhaps anterior premolars; 3) wear striations on both sides of the incisor blade often extending ventrally along the surface of the blade; and 4) gracile incisors with laterally compressed roots. Puncturing-splitting incisors can be characterized by: 1)

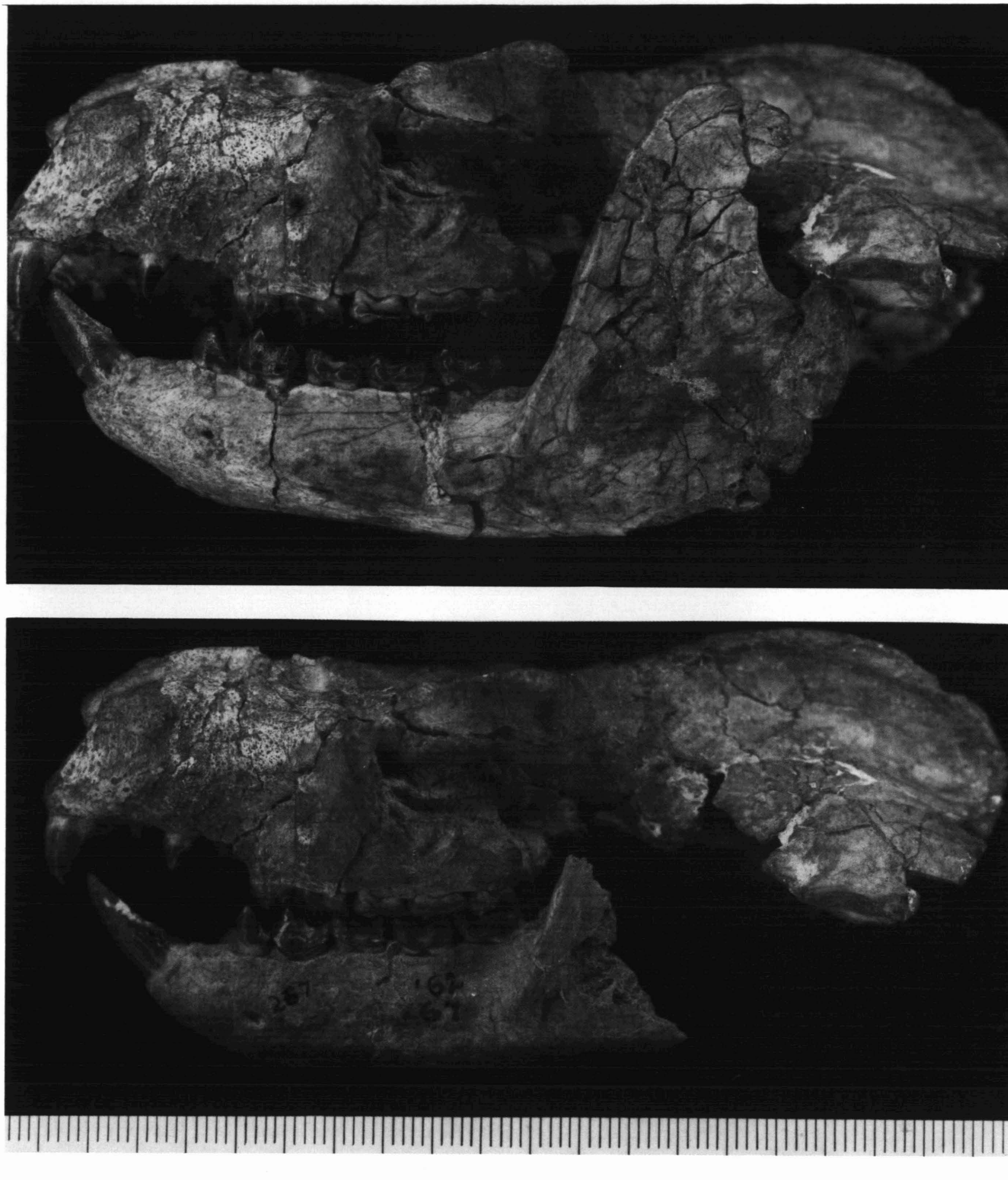

Figure 49. Occlusal relationships in *Megadelphus lundeliusi*. Top: incisors in occlusion (Skull, AMNH 55284; lower jaw, AMNH 55285). Bottom: cheek teeth in occlusion (Skull, AMNH 55284; lower jaw, AMNH 93638).

being more vertically implanted, less procumbent, more projecting with tips extending above the plane of the cheek tooth series; 2) having incisor blades dorsal-ventrally aligned, but not as open buccally, dorsal bulge less well developed; 3) showing wear striations predominantly at the tips of the incisors; and 4) being more robust with less laterally compressed roots.

The Paleocene palaechthonid *Plesiolestes* I_1 is known from a few specimens from Rock Bench Quarry in Wyoming, and the anterior upper dentition (C^1-P^2) is poorly preserved in a *Plesiolestes* specimen from the San Juan Basin in New Mexico. The lower incisor has a mixture of various features from both types described above. I_1 is more vertically implanted (approximately 35 degrees) than is typical in *Microsyops* and the tip of that tooth extends slightly above the plane of the cheek tooth series. The blade of the incisor is somewhat dorso-ventrally oriented and is open buccally. There are no wear striations except at the very tip of the incisor. I_1 is robust and only weakly laterally compressed at its roots. UKMNH 9557 preserves the upper canine roots of a specimen of *Plesiolestes nacimienti*. The canine is double rooted and is somewhat laterally compressed, but not strikingly so as in *Microsyops*. The apical wear on I_1 and the fact that it projects above the plane of the cheek tooth series suggest that this tooth was used to puncture food items instead of to slice them. However, the blade is open buccally and there is a very slight dorsal bulge. These features suggest that some limited slicing along the blade may have occurred as well. The puncturing mechanism of *Plesiolestes* was apparently less efficient than that in *M. lundeliusi*, and some degree of slicing may have occurred, although this was not the predominant function of I_1 in *Plesiolestes*.

Palenochtha, another small palaechthonid from the middle Paleocene differs from *Plesiolestes*. The I_1 of *Palenochtha* is preserved in PU 14786, a left mandible from Rock Bench Quarry. The incisor is somewhat broken but is a very procumbent tooth whose tip would not have extended above the plane of the cheek tooth series. The incisor blade is oriented dorsal-ventrally, is slightly open buccally and has a small dorsal bulge. There are wear facets along the buccal border of the blade (the lingual surface is not well enough preserved to tell anything about the wear striations) and the incisor is quite gracile with strongly compressed roots. *Palenochtha* has a slicing incisor morphology quite similar to that of *Microsyops*, but differing in the less well developed dorsal bulge and in being less open dorsally. No upper dentitions of *Palenochtha* are known in which the relevant teeth are preserved which would further define the function of the incisor. However, I believe that its dominant function was one of slicing instead of puncturing food.

Later Paleocene *Navajovius* also has an incisor morphology that indicates that its dominant function was one of slicing and shearing. I_1 is procumbent, does not project above the tooth row, has the blade dorso-ventrally oriented, but open buccally with a small but distinct dorsal bulge. It is gracile in proportions and has a laterally compressed root. The upper canine is known and it is very blade-like and laterally compressed, confirming the slicing and shearing nature of the anterior dentition of *Navajovius*.

The early Eocene diminutive microsyopid *Niptomomys* shares the same incisor features as *Navajovius*. However, *Niptomomys* is similar to *Microsyops* in having a more distinctive dorsal bulge than *Navajovius*. Other Paleocene and Eocene diminutive taxa confirm (or, at least, do not refute) the dominant trend towards incisor slicing in microsyopids, where known.

It is suggested here that the typical incisor morphology, common in varying degrees to all microsyopids, was the result of selection for a slicing-shearing anterior dentition, derived from a more puncturing-splitting anterior dentition, which is here viewed as the primitive condition. *Plesiolestes* is not far removed from the primitive morphotype, while *Palenochtha* and the Paleocene and Eocene microsyopids are more derived towards this type of anterior shearing mechanism. *Megadelphus lundeliusi* has secondarily developed a puncturing-splitting type of anterior dentition from the *Microsyops* type.

MOLAR FUNCTION

Teeth can be viewed as geometric designs made up of points (cusps), lines (crests), and planes (planar surfaces). Each of these geometric entities serves a specific function (although these functions are perhaps only partially distinct on each tooth surface) during the masticatory cycle. Cusps or points contacting one another serve to puncture or split food objects, crests or lines passing by one another serve to slice or shear food, and planar surfaces passing across one another serve to grind food into digestible pieces. The purpose of the mammalian dentition is to reduce food to a size and surface area suitable for the remaining digestive processes to extract nutrients without expending excessive amounts of energy in the process. Depending on the types of foods utilized, tooth morphologies often reflect the most efficient (or, at least, an efficient) means of reducing that food resource to usable size.

The relative amounts of tooth surface devoted to any one aspect of this trichotomy can be roughly used to sort mammals into dental categories and can provide information concerning dietary preferences. The occlusal relationships between the various components of upper and lower dentitions can provide further clues to the dominant functions of mammalian teeth.

Mammalian molar teeth are generally (not always) rather complex entities which occlude in a precise manner during the masticatory cycle. The mammalian chewing cycle can be divided into three phases or stages. The first is an initial preparatory stage in which food is gathered and punctured into small pieces. This stage corresponds to Gingerich's (1974, 1976) orthal retraction (formed by an upward and backward movement) event, although I believe that an orthal extension event (upward and slightly forward) is characteristic of some preparatory jaw movements (particularly in those mammals that use enlarged incisors to puncture and split food items).

Phase II (buccal phase of Mills, 1955, 1963; phase I of Kay and Hiiemae, 1974a) is the onset of the major portion of the chewing cycle (see Figure 50 for a diagramatic representation of phases II and III). During phase II, the mandible moves from a slightly buccal position (relative to the maxilla) upward and forward into occlusion. During this stage the crests of the molar teeth pass by one another, producing the slicing or shearing component of the cycle. Phase III occurs as the mandible moves out of centric occlusion in a downward, slightly forward and lingual direction, drawing the planar surfaces across one another and producing the crushing and grinding action of the molars.

Tables 24 and 25 summarize the results of an examination of tooth function during phases II and III for six plesiadapiform taxa. The three Paleocene genera (*Plesiolestes*, *Palaechthon*, and *Eudaemonema*) appear to be specialized for a predominantly shearing dental function throughout phases II and III, with some evidence (in *Plesiolestes* and *Palaechthon*) of puncturing as well. *Microsyops* and *Craseops* appear to retain a rather generalized dental function of shearing in phase II and grinding in phase III, with *Microsyops* somewhat more specialized for shearing and *Craseops* somewhat more specialized for crushing and grinding. *Megadelphus lundeliusi* can be characterized as predominantly a crushing and heavy shearing form.

The quantification of relative shearing and crushing surfaces is important in order to avoid arbitrary assessments of tooth morphology. In an attempt to quantify such morphological attributes, I have made over 3000 molar tooth measurements on 816 fossil plesiadapiform and primate specimens from the Paleocene and Eocene of North America. The sample represents 75 different species. Comparisons are made on the family level.

Figure 51 shows the measurements taken on each of the lower molar teeth. First, maximum length and width measurements of each lower molar were taken. Then to quantify shearing potential, five additional measurements were taken on each molar. A is the length of the paracristid; B is the length of the protocristid; C is the length of the oblique cristid; D is the length of the postcristid; and E is the length of the entocristid. All of these lengths were summed (all three molars together) and divided by the summed length of the three lower molars combined to give an estimate of shearing potential relative to tooth length for each specimen.

A similar method was used to estimate the crushing potential. G is the area of the trigonid basin, and H is the area of the talonid basin. These two areas were summed for each tooth, and then all three areas added together and divided by the summed area of all three molars to give an estimate of crushing area relative to tooth area. Natural logs of both shearing and crushing estimates were used to construct the figures.

Figure 52 shows the results of estimated shearing potential for seven families of plesiadapiforms and primates. The plesiadapiforms included Palaechthonidae, Microsyopidae, Carpolestidae, Plesiadapidae, and Paromomyidae, and primates included Adapidae and Omomyidae (see Appendix I for species and measurements from each family). The abscissa is the natural log of relative shearing potential, and the ordinate represents Land-Mammal Ages (Torrejonian, Tiffanian, Clarkforkian, Wasatchian, Bridgerian, and Uintan). The family mean for each land mammal age is represented by a dot, and the dots for each family are connected by lines. The vertical lines in each graph separate significantly differing groups based on t-tests at the .05 level.

In the lower graph, palaechthonids, microsyopids, and paromomyids have significantly greater shearing potential than either carpolestids or plesiadapids. Microsyopids maintain a significantly greater amount of shearing potential than adapids and paromomyids throughout the Eocene but are approached by omomyids in the middle and later Eocene. Figure 53 shows crushing potential plotted in the same fashion as Figure 52. In the lower graph, paromomyids have a significantly greater crushing potential than any of the other families. Palaechthonids and plesiadapids do not differ significantly, although palaechthonids do have relatively less crushing potential than plesiadapids. Microsyopids and carpolestids have significantly less crushing potential than any of the other Paleocene and early Eocene taxa. In the upper graph, microsyopids, adapids, and omomyids do not differ significantly from one another in crushing potential, however microsyopids have relatively less grinding potential than do the euprimate families. Again paromomyids have significantly greater crushing potential than do the other Eocene families.

Figure 54 plots the relative shearing potential against relative crushing potential for the Paleocene and Eocene taxa.

The first notable observation is the outlying positions of carpolestids and paromomyids. Carpolestids can be characterized as being low in both relative shearing and relative crushing potential, while paromomyids are characterized by high relative crushing potential. Carpolestids have a specialized, enlarged blade-like lower fourth premolar (see Rose, 1975b). This represents a highly specialized shearing dentition but is not reflected in the molars as P_4 dominates the functional portion of the cheek tooth series. Paromomyids also have a specialized puncturing P_4 (see Gingerich, 1974) and have concentrated shearing and especially crushing functions in the molar series.

The next notable thing is that palaechthonids and microsyopids do not differ significantly in either shearing or crushing potential and both together can be characterized as having more shearing potential and less crushing potential than adapids, omomyids, or plesiadapids. The other three families do not differ significantly in crushing poten-

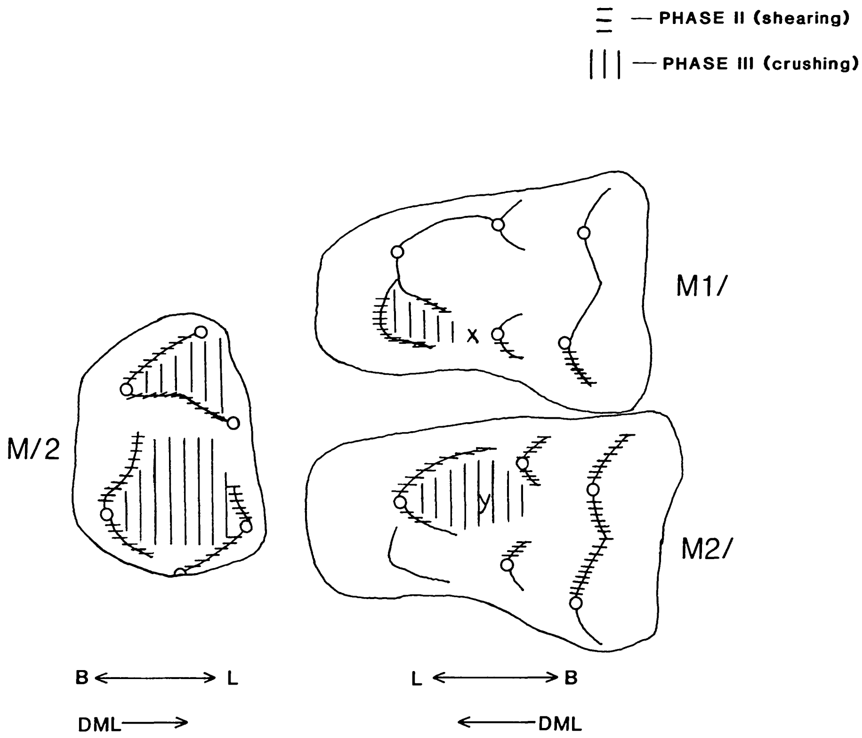

Figure 50. Shearing and crushing surfaces that are utilized in a generalized mammal as left lower M_2 passes across left upper M^{1-2}. Phase II shearing occurs as the teeth come into centric occlusion. Phase III crushing occurs as the teeth pass out of centric occlusion to begin a new chewing cycle. X and Y represent positions of M_2 protoconid and hypoconid on upper molars when teeth are in centric occlusion. Abbreviations: B = buccal, L = lingual, DML = direction of movement of lower jaw.

tial, but are arrayed in a continuum from least shearing potential (adapids) to most shearing potential (omomyids). The relatively high shearing potentials exhibited by microsyopids and palaechthonids confirms the observations made above concerning their morphology and occlusal relationships. Microsyopids in general can be characterized as having dentitions which emphasize the shearing component of dental function and place less emphasis on the crushing and grinding component.

Table 24. Phase II Dental Function (Abbreviations:protocone-pr; paracone-pa; metacone-mt; hypocone-hy; postprotocingulum-ppc; paraconule-prc; metaconule-mtc; protoconid-prt; paraconid-pac; paracristid-pacr; metaconid-mtd; hypoconid-hyc; entoconid-enc; hypoconulid-hyd; talonid notch-tn; postvallid-pv; mesoconid-med; ectoflexid-ecx; hypoconulid notch-hn; postcristid-psd; trigonid notch-trn; prevallid-prv; postmetacrista-pmcr; preparacrista-ppcr; preprotocrista-prrc; trigon notch-tgn; mesostyle-mes; premetacrista-prmc; postprotocrista-psrc; hypoflexid-hyx; posthypocrista-phcr; oblique cristid-oc; posterior shearing mechanism-PSM; trigon basin-tgb).

Taxon	Protocone	Paracone	Metacone	Hypocone PPC	Paraconule	Metaconule	Protoconid	Paraconid Paracristid	Metaconid	Hypoconid	Entoconid Hypoconulid
Plesiolestes	shears on tn	punctures on mtd shears on pv	punctures on hyc shears in hn/pacr	shears/ crushes on pacr	shears on mtd/trn	shears in hn	punctures on pa shears on prv/ppc	punctures on mt shears on ppc	punctures on pa shears on prrc/prc	punctures on mt shears on tgn	shears on ppc
Palaechthon	shears in tn	punctures on mtd shears on pv	punctures on hyc shears on psd	shears/ crushes on pacr	shears on mtd/trn	shears on psd/pac	shears on pmcr/mtc/ pacr	shears on pmcr	punctures on pa shears in prrc/prc	shears in tgn	shears on posterior pr
Eudaemonema	shears in tn	shears on pv/med	shears on psd/prv/ pacr	shears on pacr	shears on pv	shears on prv	shears on pmcr	punctures on mt shears on pmcr	shears on pmcr/ppcr	shears in tgn/mes	shears on posterior pr
Microsyops	shears in tn	shears on pv/ecx	shears on psd/hyd	weak shear on pacr	shears on pv/tn	shears on psd	shears on ppcr/prc	shears on pmcr	shears in ppcr/prc	shears in tgn	shears on mtc/prmc/ pscr
Megadelphus lundeliusi	weak shear in tn	punctures on mtd crushes on mtd	crushes on psd	crushes on hyd/psd	crushes on pr/pv	shears/ crushes on ppcr	shears crushes on pmcr	punctures on pa crushes on pa/pv	shears in tgn	crushes on mt	
Craseops	shears in tn	punctures on mtd shears on pv	shears on pacr	none	shears on pv	absent	shears on pprc/prc	shears on pmcr	punctures on pa shears on prc/pv	shears in tgn/mes	punctures on mt shears on prmc

BODY SIZE

The morphology of mammalian teeth can indicate a great deal about how they are used to process food. Another aspect which makes them particularly useful in reconstructing dietary preferences of fossil mammals is the role they can play in predicting body weight. Body size is an important factor in the type of diet that an animal utilizes. Small bodied forms with relatively high metabolic rates require high energy foods rich in protein, while larger bodied forms with lower metabolic activity can live on lower energy foods. Abundance of food and the amount of energy expended in the search for and acquisition of food items also plays a role in dietary determination. Small mammals, including many small primates, rely on high energy foods such as insects, which require time to seek out and capture, but the benefits gained are a rich source of protein. Larger bodied primates, such as gorillas, could conceivably eat an insect rich diet, but the energy requirements for finding and eating enough insects to provide minimum nutrients are too high for such a large body size. Instead, gorillas eat less nutrient rich, but far more abundant, leaves, flowers, and other vegetable matter.

Kay (1975) found that living primates under 500 grams in body weight were primarily insectivorous in dietary habit. Above this body weight, primates tend to be more frugivorous and less insectivorous, and in larger body weight ranges more folivorous than frugivorous. Gingerich, et al. (1982) termed the 500 gram boundary as Kay's threshold.

Gingerich, et al.(1982) and more recently Gingerich and Smith (1984) have provided regression formulas for predicting body weight based on tooth size. These regression formulas are based on the relationships between tooth size

Table 25. Phase III Dental Function (Abbreviations as in Table 24).

Taxon	Protocone	Paracone	Metacone	Hypocone PPC	Paraconule	Metaconule	Protoconid	Paraconid Paracristid	Metaconid	Hypoconid	Entoconid Hypoconulid
Plesioletes	crushes on hyc shears on hyc/med	none	none	shears/ crushes on pacr	crushes on med shears on med/pv	none	shears on prrc crushes on pv	shears on ppc	shears on prrc	crushes on tgb	shears on ppc
Palaechthon	shears on med/hyc	none	none	shears/ crushes onpacr	crushes onmed	none	shears/ crushes onppc	shears on ppc	shears on prrc	shears on mtc/psrc	shears on posterior pr
Eudaemonema	shears on med/hyc	none	none	shears on prv/pacr	shears on pv/med	shears on prv	shears on phcr	shears on phcr	shears on phcr/pr	oc shears on pscr	PSM
Microsyops	crushes on hyc	none	none	PSM	shears on pv	shears on hyc/prv	shears on prrc/pv	weak shear on phcr	shears on prrc	crushes in tgb	PSM
Megadelphus lundeliusi	crushes on hyc/ hyx	none	none	weak crushing on psd	crushes on pv	crushes on prv	crushes on prrc	crushes on prmc	crushes on prrc	crushes on pr	crushes on psrc
Craseops	crushes on hyc shears on hyc/med	none	none	none	shears on pv	absent	shears on prrc	weak crushing on hy	weak crushing on prrc	crushes on pr oc shears on prc/pr	shears/ crushes on psrc

and body size in modern primates (Gingerich, et al., 1982) and in modern primates and insectivores (Gingerich and Smith, 1984). By using these formulas, it is possible to estimate average body weights in fossil primates and closely related forms such as plesiadapiforms.

Figure 55 presents body weight estimates for 79 species of plesiadapiforms and fossil primates using regression formulas from Gingerich, et al. (1982). The abscissa is the natural log of body weight in grams and the ordinate is the number of species in each body weight interval. Body weights are estimated for each of the land mammal ages from Torrejonian at the bottom through Uintan at the top. The unshaded areas represent primates, the shaded areas plesiadapiforms, and the cross-hatched areas palaechthonids and microsyopids (Appendix II provides measurements for the taxa used to construct Figure 55). The vertical line down the center of the figure represents Kay's threshold of 500 grams. 95% confidence intervals were calculated for all species and only those whose confidence intervals fall at or below 500 grams were included to the left of the threshold.

In the Torrejonian all of the palaechthonids (and 80% of all the species) except *Torrejonia wilsoni* are below the 500 gram threshold. In the Tiffanian, the same holds true with only *Torrejonia sirokyi* above the threshold. In the Clarkforkian, *Arctodontomys simplicidens* is slightly above the threshold while in the Wasatchian, *Microsyops latidens* and *Microsyops scottianus* fall slightly above the threshold. In the Bridgerian and Uintan, all microsyopids (except *Alveojunctus* in the Bridgerian and *Uintasorex* in the Uintan) fall well above Kay's Threshold. Most palaechthonids were small bodied forms, while microsyopids are split into medium and larger bodied microsyopines and the diminutive uintasoricines, navajovines, and micromomyines. The division between these two body size categories is apparent in the Tiffanian and may well be present in the Torrejonian.

Of the other plesiadapiforms, carpolestids and paromomyids remain fairly small throughout, while plesiadapids become larger. The primates of modern aspect appear in the Wasatchian in two distinct body size ranges and for the most part remain distinct throughout the Eocene, with omomyids representing the small radiation and adapids representing the larger radiation.

Table 26 summarizes the information concerning incisor function, molar morphology, occlusion, estimated body weights, and quantitative analysis of the groups discussed above.

For the palaechthonids *Plesiolestes* and *Palaechthon* the incisors were of a puncturing type and the molar series was a puncturing-shearing type. It should be noted here that puncturing is the one aspect of dental function that is difficult to quantify because puncturing occurs at points (cusps), which by definition have no length or surface area. Beyond counting the number of places where puncturing occurs, little quantitative analysis can be carried out. *Plesiolestes* appears to have been capable of more puncturing and more efficient shearing than *Palaechthon*, but both taxa are, for the most part, oriented towards shearing. Both taxa are below 500 grams estimated body weight (110 to 150 grams for *Palaechthon* and 275 to 310 grams for *Plesiolestes*). Palaechthonids were surely highly insectivorous. Puncturing-piercing incisors are useful for catching insects and in initially puncturing the hard exoskeletons. Further puncturing and shearing by the molars reduce the insects to digestible pieces. Little grinding or crushing is needed to digest the soft inner bodies of insect prey.

Eudaemonema also was probably highly insectivorous. If its incisor was similar to that of *Mixodectes* (see Szalay, 1969b) it would have been of a puncturing-piercing type

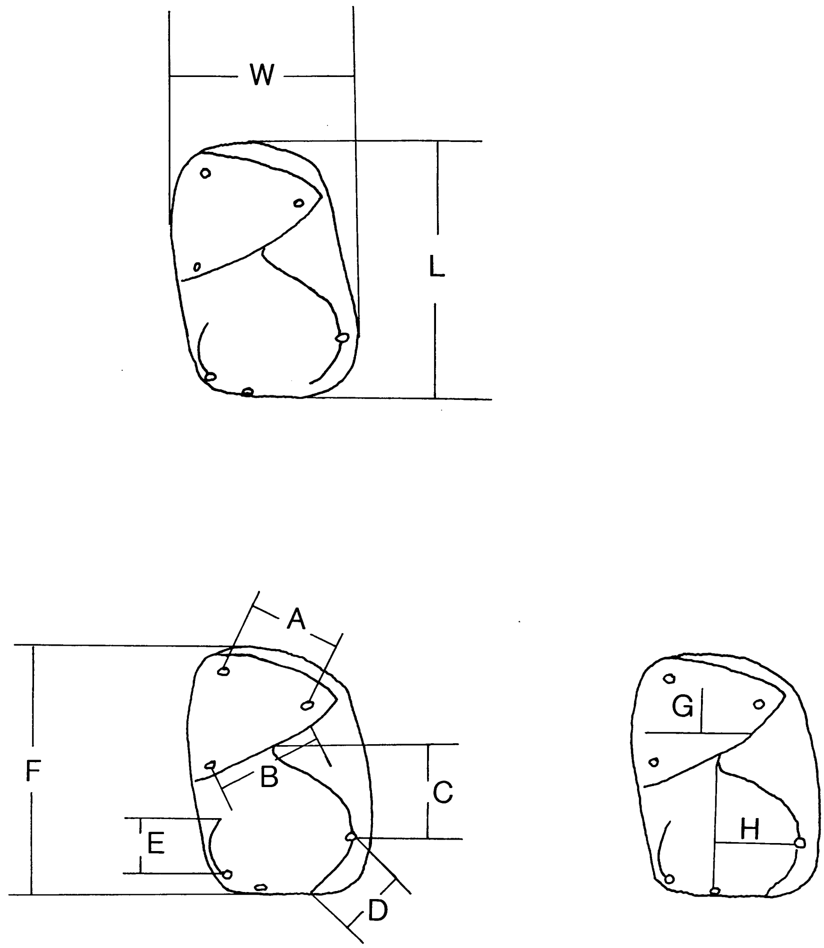

Figure 51. Tooth quantification measurements taken on plesiadapiform and primate taxa. Abbreviations: A-paracristid length; B- protocristid length; C- oblique cristid length; D- postcristid length; E- entocristid length; F- total length; G- trigonid basin area; H- talonid basin area; L-maximum length; W- maximum width.

as well. The specialized shearing dentition of *Eudaemonema* was an efficient insect processing tool as well. Estimates of body weight for *Eudaemonema* are somewhat higher than Kay's threshold, approximately 800 grams (body weight estimates for *Mixodectes* range from 900 to 1700 grams). It must be remembered that Kay's threshold is based only on insectivorous living primates. Plesiadapiforms may not reflect the same adaptations as other primates so that direct dietary comparisons may not be valid. True insectivores reach sizes well above 500 grams (*Tenrec*, the largest living insectivore, reaches body weights in excess of 1500 grams), and perhaps an upper limit on insectivory should be raised to 1500–1600 grams for these early taxa, particularly where tooth morphology suggests that shearing was the dominant dental function.

Microsyops has procumbent, lanceolate, slicing lower incisors, a shearing molar dentition and a wide range of body weights. Body weight estimates for *Microsyops* range from 700 grams for *M. cardiorestes* to over 3000 grams for *M. kratos*. All *Microsyops* species except *M. annectens* and *M. kratos* are at or below 1500 grams in estimated body weight. For all of these smaller species, an insectivorous diet is likely. The procumbent, slicing incisors would have proved useful in slicing and cutting insect bodies, as would the shearing molar adaptations. It is possible that *Microsyops* specialized on softer bodied insect prey (such as larvae) instead of those with hard chitinous exoskeletons. *Microsyops annectens* and *Microsyops kratos* were probably too large bodied to have been specialized entirely on insects. Some *Microsyops annectens* specimens (for example, AMNH 12595) show signs of developing heavier phase III wear facets (as in *Megadelphus lundeliusi*, but

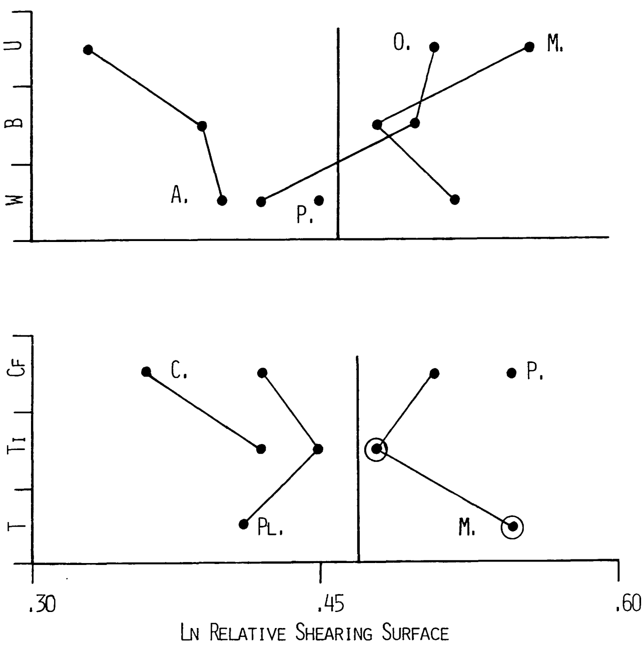

Figure 52. Shearing surfaces in plesiadapiforms and primates. Abscissa represents the natural log of relative shearing surface. Ordinate represents land mammal ages from Torrejonian through Uintan. Closed circles represent family means for each land mammal age in which a family is represented. Open circles around closed circles represent palaechthonids. Abbreviations: A- adapids; C- carpolestids; M- microsyopids; P- paromomyids; PL- plesiadapids. Solid vertical lines separate significantly (at the .05 level) different families.

not as well developed) than is typical for other smaller *Microsyops* species. This indicates that heavier shearing and particularly crushing of harder food objects had become an important part of dietary preparation in *M. annectens*. These harder food objects may have taken the form of fruits and nuts, in particular nuts that also are high in nutrient value. The single *M. kratos* specimen does not show this characteristic phase III wear, but the specimen is a juvenile so wear facets were not yet well formed. If the estimated body weight (over 3000 grams) for *M. kratos* is correct, that species probably supplemented its insect diet with other foods as well.

Megadelphus lundeliusi can be characterized as having a procumbent-projecting, puncturing lower incisor; shearing-grinding molars with heavy, cupped phase III wear facets; and body weights in excess of 4000 grams. *Megadelphus lundeliusi* probably concentrated on hard, tough food objects such as nuts and small fruits. Smith (pers. comm.) has suggested that this type of heavy, cupped wear is typical of terrestrial mammals that incorporate large quantities of abrasive grit into their diets. It is possible that part of the diet of *M. lundeliusi* consisted of roots and rhizomes dug up from the ground. *Megadelphus lundeliusi* may have supplemented its diet with some insects, but they were probably not the major dietary element that I have inferred for *Microsyops*.

Craseops has shearing-grinding molars and a body weight of at least 5000 grams. It too probably ate foods other than insects. The small sample of teeth indicates that phase II shearing wear was quite well developed, while phase III crushing wear was less well developed. This suggests that softer food objects, such as fleshy fruits may have been the major dietary component of *Craseops*.

A wide variety of dietary regimes were utilized by microsyopids, ranging from strict insectivory in palaechthonids, to modified insectivory in smaller *Microsyops* species, to frugivory in *Craseops* and omnivory in the larger species of *Microsyops* and *Megadelphus*. Other food sources may also have been utilized, such as saps and gums. The procumbent lower incisors would have been a useful tool for prying up tree bark in search of these high energy foods.

PLESIADAPIFORMES-PRIMATE DENTAL RELATIONSHIPS

Gingerich (1976) and Bown and Rose (1976) argued for the inclusion of Plesiadapiformes in the order Primates. Gingerich (1976) included plesiadapiforms in primates based on the following reasons. First, although most of the better known plesiadapiform species (for example, *Plesiadapis tricuspidens*) were highly specialized taxa, their middle Paleocene ancestors were more generalized forms. Second, the first primates of modern aspect (Tarsiiformes and Lemuriformes) can be traced back in the fossil record to the earliest Eocene where they suddenly appear in mammalian faunas "probably due to northward migration with the subtropical climatic belt expanding at that time," (see Gingerich, 1976, page 101). Third, the only mammals known during the Paleocene that resemble these primates of modern aspect are plesiadapiforms. Gingerich (1976) particularly noted the resemblances between early tarsiiforms and plesiadapiforms (similar molar structures, enlarged incisors, and ossified auditory tubes). He used these features to link these taxa in his suborder Plesiotarsiiformes. Gingerich (1981, 1984), has subsequently questioned this relationship and now feels that there are no close affinities between Tarsiiformes and Plesiadapiformes. Lemuriformes have no apparent ancestor among the Paleocene taxa except possibly *Purgatorius* (Gingerich, 1976). However, Gingerich (1976) instead noted the resemblances between early lemuriforms and the first known fossil anthropoids from the early Oligocene of the Fayum Depression in Egypt. Gingerich grouped these taxa in the suborder Simiolemuriformes.

The earliest known tarsiiforms are from early Wasatchian equivalent beds at Dormaal in Belgium (*Teilhardina belgica*). The earliest known adapids, *Donrussellia provincialis* and *Cantius torresi*, are from Rians in France and the Clark's Fork Basin in Wyoming, respec-

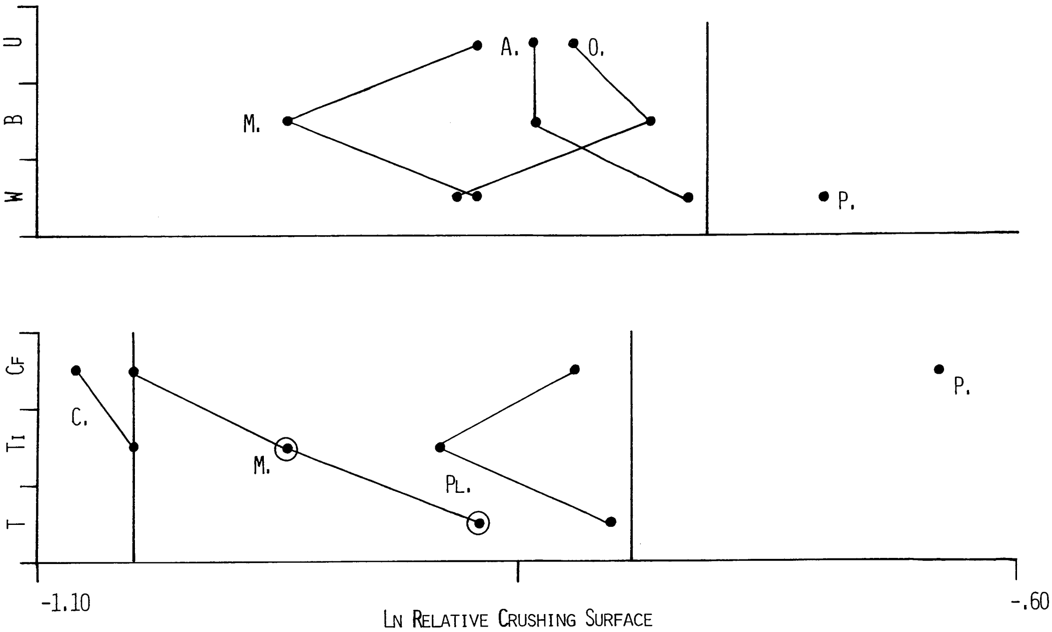

Figure 53. Relative crushing surfaces in plesiadapiforms and primates. Abscissa represents the natural log of relative crushing surfaces. Ordinate represents land mammal ages from Torrejonian through Uintan. Closed circles represent family means for each land mammal age in which a family is represented. Open circles around closed circles represent palaechthonids. Vertical lines separate significantly (at the .05 level) different families. Abbreviations as in Figure 52. See text for further discussion.

tively. Dental comparisons of these taxa with plesiadapiforms reveal only overall similarities that either primitive retentions or convergent similarities. The incisor region of the three taxa is virtually unknown. Szalay (1976) and Szalay and Delson (1979) indicated that the incisors of *Teilhardina belgica* were not enlarged. *Teilhardina americana*, the earliest North American tarsiiform, may have had slightly enlarged central incisors (Bown and Rose, 1987). These interpretations differ from that of all known plesiadapiforms (with the possible exception of *Purgatorius*). Relatively large canines are present in *Teilhardina* and *Donrussellia* (see Godinot, 1981), a trait also shared by plesiolestines. However, the canine is also relatively large in *Purgatorius* so that this is probably a primitive retention in *Teilhardina* and *Donrussellia*.

A lower first premolar (P_1) is retained in *Donrussellia* (Godinot, 1978, 1981) and is apparently present in at least some *Teilhardina* specimens. Retention of P_1 makes both species more primitive than any plesiadapiform except *Purgatorius* (and perhaps *Palenochtha weissae*) and indicates that no known plesiadapiform species (except for *Purgatorius*) could have led to either Eocene taxa.

Figure 56 shows the results of a PAUP analysis (Swofford, 1985) run on 14 taxa of fossil dermopterans, plesiadapiforms, and euprimates. The analysis is based on 17 dental characters (Table 27) with each character weighted equally to avoid over emphasis of characters with multiple states. A cladogram of possible relationships is presented in figure 56. The cladogram is derived from the consensus tree for these taxa. The branch and bound option of PAUP was employed to assure that the most parsimonious tree was found.

Most of the relationships that have been suggested throughout this work are supported by this analysis. Although euprimates (*Cantius* and *Teilhardina*) are described as sister taxa to the dermopteran-plesiadapiform clade, the suggested shared, derived characters (see figure caption) are all likely to be homoplasic. I believe it unlikely that either group of euprimates shares sister taxon status with the dermopteran-plesiadapiform clade.

In terms of body size and relative shearing and crushing surfaces, *Teilhardina* and *Donrussellia* are distinctive from other primates of modern aspect. The estimated body weight of *Teilhardina* is 90 grams, while that of *Donrussellia* is 200 grams, both well below Kay's threshold. Thus, both were likely to have been insectivorous.

The relative shearing and grinding surfaces for the two taxa are plotted in Figure 57 comparing them with the taxa discussed above. Both have relative crushing surfaces below any of the other taxa and indicate that little if any crushing was being carried out during mastication. In terms of relative shearing surfaces, the two taxa appear to differ

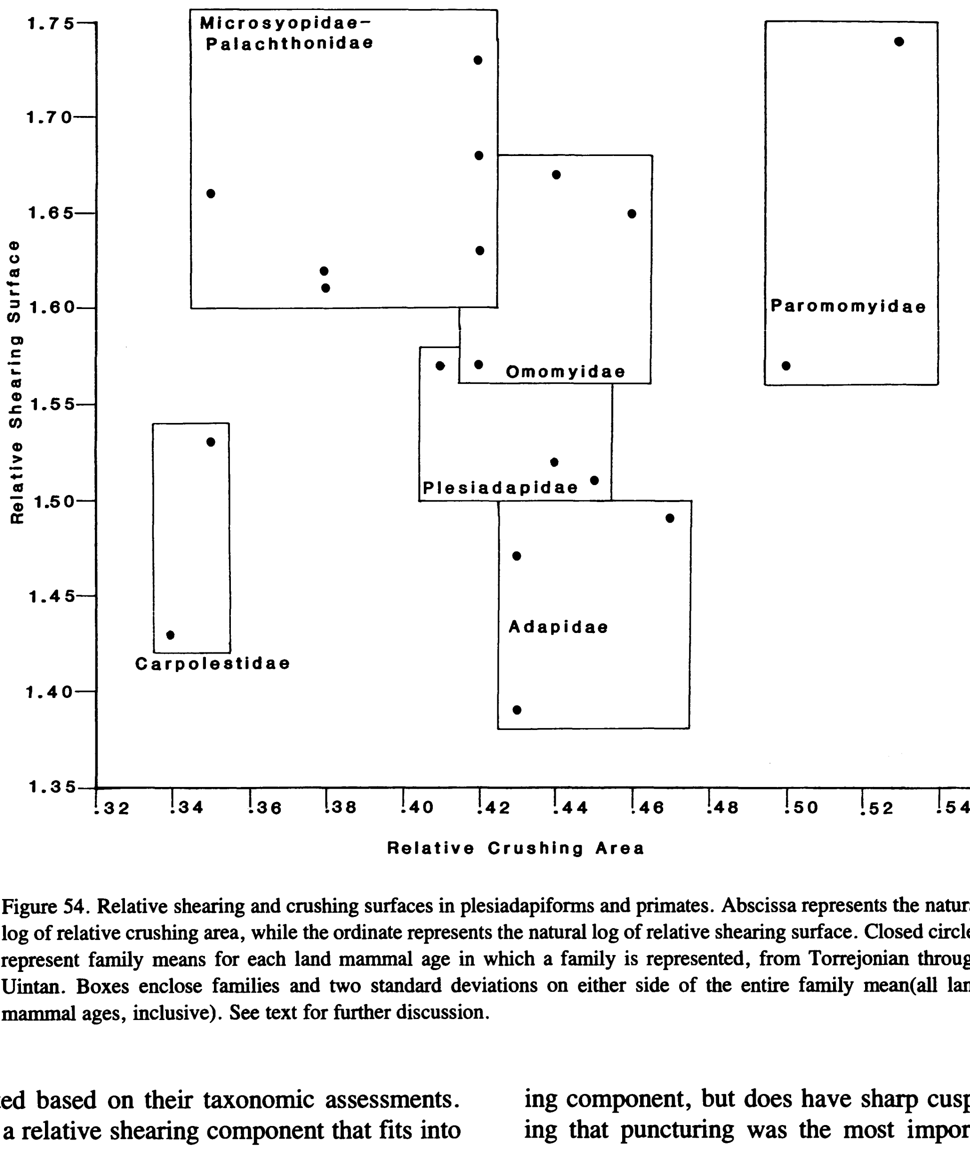

Figure 54. Relative shearing and crushing surfaces in plesiadapiforms and primates. Abscissa represents the natural log of relative crushing area, while the ordinate represents the natural log of relative shearing surface. Closed circles represent family means for each land mammal age in which a family is represented, from Torrejonian through Uintan. Boxes enclose families and two standard deviations on either side of the entire family mean(all land mammal ages, inclusive). See text for further discussion.

from the expected based on their taxonomic assessments. *Teilhardina* has a relative shearing component that fits into the range of adapids, while *Donrussellia* has relative shearing surfaces which place it within omomyids and microsyopids. In both cases, the small body size probably plays a role in the relative importance of each parameter.

Teilhardina has a shearing component similar to adapids, but it differs greatly in relative crushing and in body size. The average adapid plotted on the graph weighs in excess of 2400 grams and has a much larger crushing component to its dentition. Adapids have reduced the shearing component and increased the crushing and grinding component, and this, along with the rather large body sizes, suggests a frugivorous-omnivorous dietary regime. *Teilhardina* has a similar shearing component, but for both adapids and *Teilhardina* this component is very low indicating that this aspect of mastication was relatively unimportant. *Teilhardina* has neither a high shearing nor crushing component, but does have sharp cusped teeth suggesting that puncturing was the most important aspect of its masticatory system. This combined with extremely small size suggests a strictly insectivorous diet for *Teilhardina*, with puncturing teeth used to crack and split the chitinous exoskeletons of its insect prey.

Donrussellia is also quite small and was likely a primary insectivore. However, it has emphasized a shearing masticatory system and may, like microsyopids, have specialized on softer-bodied insect prey. Unfortunately, its anterior dentition remains unknown, so further similarities to microsyopids are unproven.

Both *Teilhardina* and *Donrussellia* are unlike any other primate or plesiadapiform in their dental specializations for shearing and crushing combined. This emphasizes their place as very early modern aspect primates and supports Godinot's (1981) contention that they are close to the initial split between haplorhines and strepsirhines, with neither

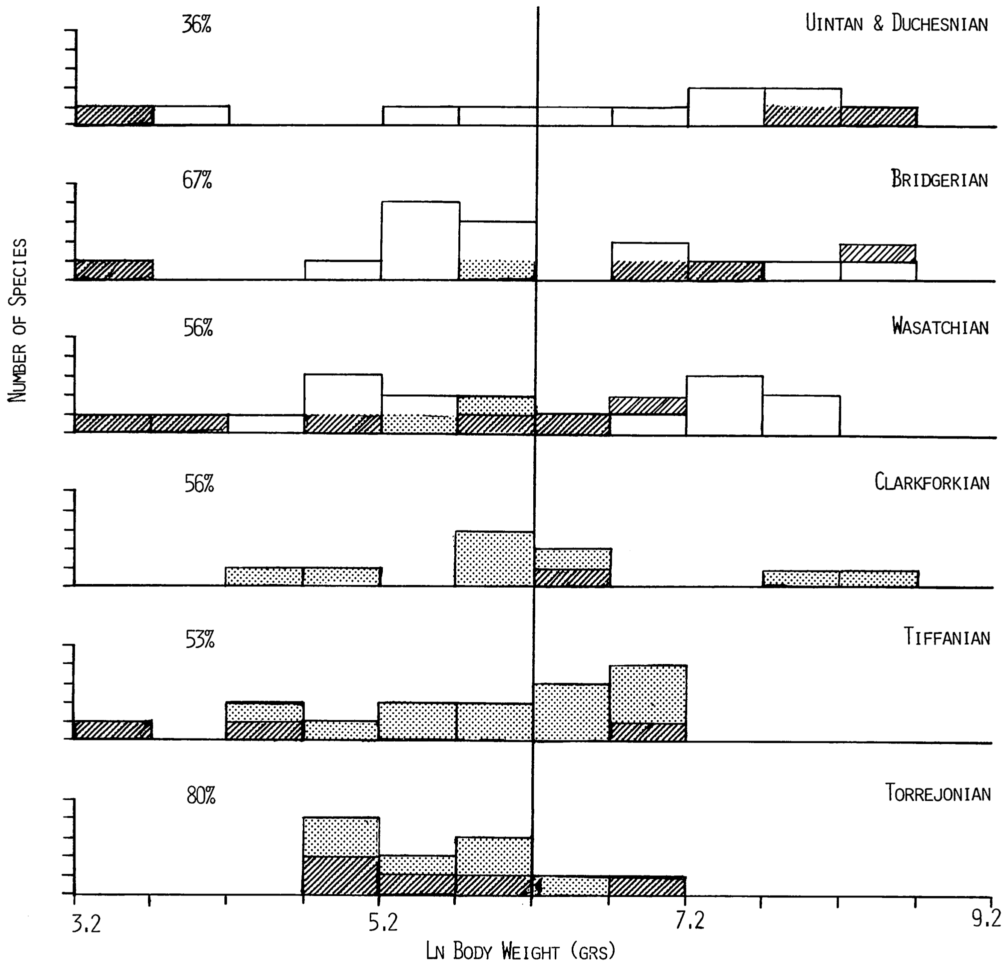

Figure 55. Body weight estimates for plesiadapiforms and primates. Abscissa represents the natural log of body weight in grams, while the ordinate represents the number of species in each body weight range for a given land mammal age, from Torrejonian through Uintan. The solid vertical line represents Kay's threshold of 500 grams. Stippled boxes represent plesiadapoids, cross-hatched boxes represent microsyopoids, and open boxes represent primates of modern aspect (euprimates). Percentage figures indicate the percentage of taxa below Kay's threshold for each land mammal age. See text for further discussion.

far differentiated from their common ancestry. Both are quite unlike any plesiadapiform and do not support a plesiadapiform ancestry for primates of modern aspect.

Table 26. Summary of dental function and estimated body weight among plesiadapiforms.

Taxon	Incisor Function	Molar Function	Molar Quantification	Estimated Body Weight
Palaechthonidae	projecting semi-lanceolate puncturing	puncturing-shearing	shearing	most under 500 grams
Eudaemonema	projecting puncturing	shearing	?	over 500 grams about 800 grams
Microsyops	procumbent lanceolate slicing	shearing	shearing	most over 500 grams
Megadelphus lundeliusi	projecting semi-lanceolate puncturing	shearing crushing	shearing	well above 500 grams (4000gr)
Craseops	?	shearing crushing	shearing	well above 500 grams (5000gr)

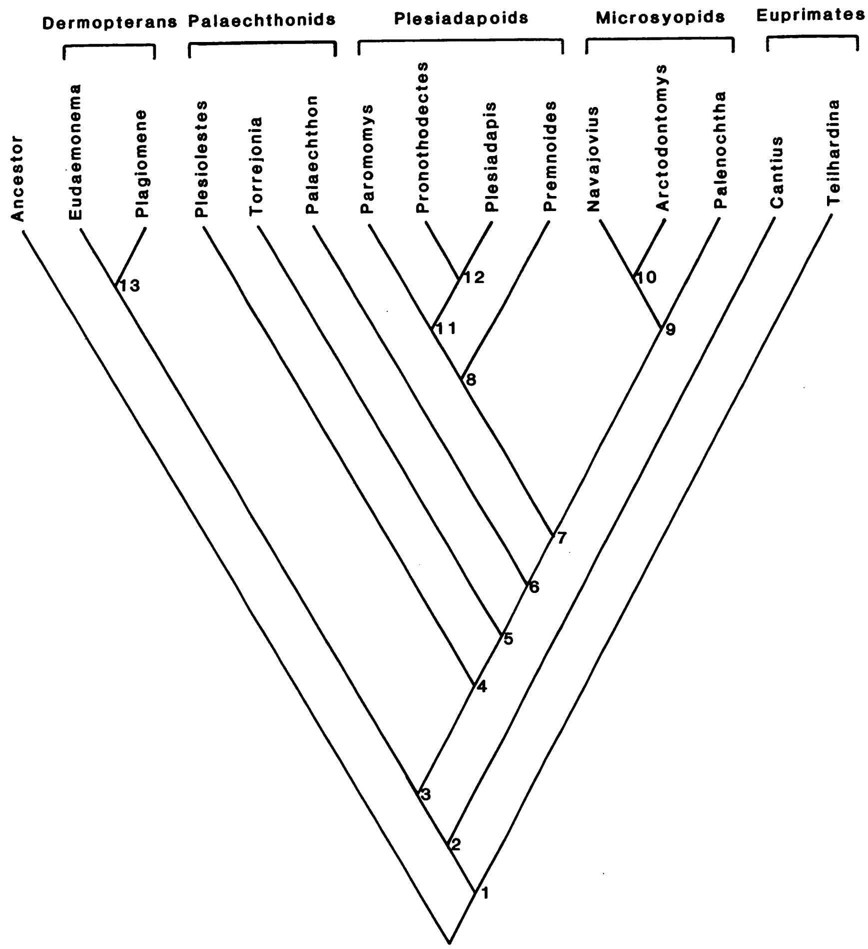

Figure 56. Cladogram of possible relationships among plesiadapiforms, fossil dermopterans, and euprimates, based on 17 dental characteristics. Cladogram is derived from consensus tree output of PAUP analysis (Swofford, 1985). *Purgatorius unio* was used to develop hypothetical ancestral condition. Shared, derived characters representative of each node are as follows: Node 1 - molar paraconid cuspate, molar cingulids present; Node 2 - P_4 metaconid small, molar trigonids compressed, molar hypocone small and formed on postprotocingulum; Node 3 - P_4 talonid 2–3 cusped, P^4 semimolariform; Node 4 - I_1 enlarged, procumbent; Node 5 -P_4 semimolariform; Node 6 - molar cingula developed; Node 7 - P_4 paraconid absent; Node 8 - P_4 talonid single cusped, molar paraconid small and bulbous; Node 9 - M(1–2) trigonids open, I_1 semilanceolate; Node 10 - I_1 lanceolate, molar hypoconulid small and twinned, molar hypocone small and not formed on postprotocingulum, molar cingula developed, P^4 premolariform; Node 11 - molar cingulids developed; Node 12 - P_4 premolariform and compressed, molar hypoflexid sloping and shelf-like; Node 13 - P_4 talonid 3 cusped, molar metaconid elevated, M^1 transverse valley strong, molar cingula strong. See text for further discussion.

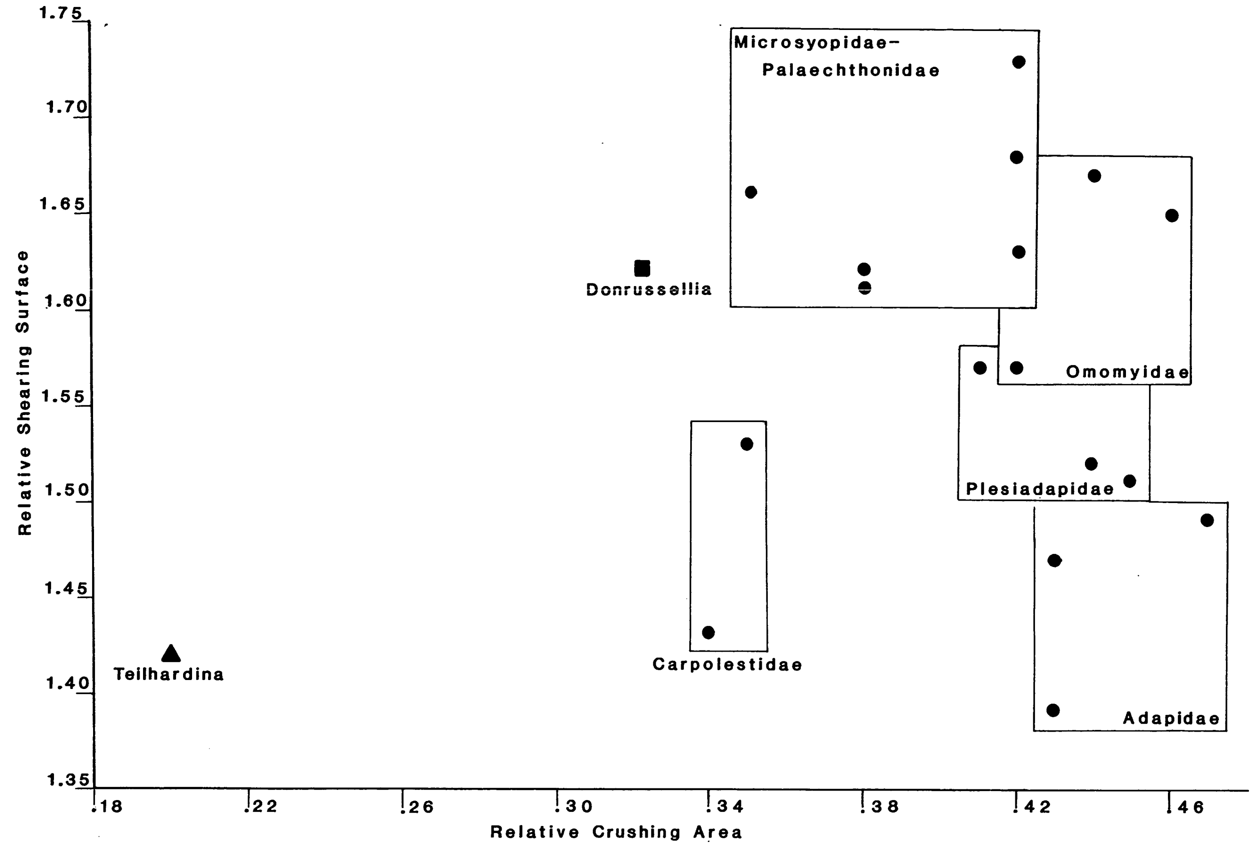

Figure 57. Relative shearing and crushing surfaces in *Donrussellia* and *Teilhardina*. Abscissa represents the natural log of relative crushing area, while the ordinate represents the natural log of relative shearing surface. Closed circles are family means from each land mammal age (Torrejonian through Uintan) in which a family is represented. Boxes enclose families and two standard deviations on either side of mean for entire family (all land mammal ages inclusive). See text for further discussion.

Table 27. Comparative dental characteristics of various plesiadapiforms, fossil dermopterans, *Cantius* and *Teilhardina* (PPC = hypocone developed on postprotocingulum).

Genus	I_1	P_3	P_4	P_4 paraconid	P_4 metaconid	P_4 talonid	Molar paraconid	Molar metaconid	Molar trigonid	Molar cingulid
Palaechthon	?	premolariform	premolariform	weak	absent	2 cusped	small cuspate	not elevated	not angled compressed	weak
Teilhardina	caniniform	premolariform	semi-molariform	weak	absent	1 cusped	cuspate	not elevated	not angled open	weak
Cantius	spatulate	premolariform	semi molariform	small cuspate	cuspate	1 cusped	cuspate	not elevated	not angled open	strong
Pronothodectes	caniniform projecting	premolariform	premolariform compressed	absent	absent	1 cusped	small cuspate	not elevated	not angled compressed	strong
Arctodontomys	lanceolate	premolariform	premolariform	absent	absent	1 cusped	small cuspate	not elevated	not angled open	weak
Eudaemonema	enlarged compressed	premolariform	semi-molariform	low shelf	cuspate	3 cusped	low shelf	elevated	not angled	weak
Mixodectes	enlarged compressed	premolariform	premolariform	weak	absent	1–2 cusped	low shelf	elevated	not angled	absent or weak
Plagiomene	bicuspate	semi-molariform	molariform	shelf-like	cuspate	3 cusped	cuspate	weakly elevated	angled	strong
Plesiolestes	semi-lanceolate	premolariform	semi-molariform	weak	low cuspate	2 cusped	small cuspate	not elevated	not angled compressed	weak
Torrejonia	?	premolariform	semi-molariform	weak	absent	2 cusped	small cuspate	not elevated	not angled compressed	weak
Paromomys	?	premolariform	premolariform	absent	absent	2 cusped	weak	not elevated	not angled compressed	strong
Plesiadapis	caniniform projecting	premolariform	premolariform compressed	absent	absent	1 cusped	small cuspate	not elevated	not angled compressed	strong
Navajovius	semi-lanceolate	premolariform	premolariform	absent	absent	2 cusped	cuspate	not elevated	not angled open	weak
Palenochtha	semi-lanceolate	premolariform	premolariform	weak	absent	2 cusped	cuspate	not elevated	not angled open	weak

Table 27. (continued)

Genus	Molar hypoconulid	Molar hypoflexid	M^1 transverse valley	Molar hypocone	Molar cingula	P^4	Lower dental formula
Palaechthon	small lingual	sloping shelf	absent	small PPC	weak	semi-molariform	2-1-3-3
Teilhardina	small lingual	sloping shelf	absent	weak not PPC	weak	premolariform	2-1-(3-4)-3
Cantius	small lingual	sloping shelf	absent	small PPC	weak	premolariform	2-1-4-3
Pronothodectes	expanded M_3	steep	absent	small PPC	strong	semi-molariform	2-1-3-3
Arctodontomys	small twinned	sloping shelf	absent	weak not PPC	weak	semi-molariform	1-0-3-3
Eudaemonema	small lingual	sloping shelf	developed	strong not PPC	very strong	semi-molariform	2-1-4-3
Mixodectes	small lingual	steep	developed	strong PPC	weak	premolariform enlarged	2-0-3-3
Plagiomene	small lingual	sloping shelf	strong	absent	strong	molariform	3-1-4-3
Plesiolestes	small lingual	sloping shelf	absent	small PPC	weak	semi-molariform	2-1-3-3
Torrejonia	small lingual	sloping shelf	absent	small PPC	weak	semi-molariform	?
Paramomys	absent	sloping shelf	absent	strong PPC	very strong	semi-molariform	2-1-3-3
Plesiadapis	expanded M_3	steep	absent	strong PPC	strong	semi-molariform	1-0-(2-3)-3
Navajovius	small twinned	sloping shelf	absent	weak not PPC	weak	semi-molariform	1-1-3-3
Palenochtha	small lingual	sloping shelf	absent	small PPC	strong	semi-molariform	1-1-3-3

VIII
CONCLUSIONS

The first question posed at the beginning of this investigation concerned the relationships of archaic North American primate-like taxa to primates of modern aspect. I have examined most of the relevant dental, cranial, and postcranial evidence available and have found that, while plesiadapiforms are similar to primates of modern aspect in many details, there is insufficient evidence to link them with these primates in any ancestral-descendant relationship. Plesiadapiforms share features with primates of modern aspect, but there is no evidence to indicate that these are anything more than either shared primitive characteristics or characters due to convergent evolution. I have chosen to retain these taxa in Primates?, recognizing them as distinct from primates of modern aspect, but also as distinct from their presumed insectivorous ancestry (see below). There closest relationships appear to be with the fossil dermopteran group, Plagiomenidae.

The second question posed here dealt with the relationships within Plesiadapiformes. Conclusions reached can be summarized as follows: 1) Paromomyidae should be recognized as a small, tightly-knit group consisting of only four genera (*Paromomys*, *Phenacolemur*, *Ignacius*, and *Elwynella*); 2) Paromomyidae should be included in the superfamily Plesiadapoidea, not Microsyopoidea; 3) the essentially late Paleocene-Eocene family Microsyopidae can be best viewed as being derived from the early and middle Paleocene family Palaechthonidae, and both families should be included in Microsyopoidea; 4) changes in paleoclimatic conditions along with competition with other groups such as rodents was the likely cause of the extinction of most plesiadapiforms at the Clarkforkian-Wasatchian boundary; 5) most microsyopoids were specialized as small insectivorous forms, although some later Eocene taxa were probably frugivorous or omnivorous; 6) microsyopids and paromomyids survived well into the Eocene because of dental specializations which allowed them to avoid direct competition with primates of modern aspect and other mammals such as rodents.

The first three conclusions are based almost exclusively on dental evidence. Further corroboration or refutation of these hypotheses must await more complete fossil material.

The paleoclimate of the Paleocene and Eocene (see Chapter III) has been reconstructed as follows. During the middle Paleocene, warm, tropical climates dominated the North American Western Interior. This climate deteriorated into a more temperate, seasonal, cooler period during the late Paleocene. By the early Eocene, the climate had again become warmer and more tropical. Superimposed on this climatic reconstruction is the paleogeographic distribution of the relevant plesiadapiform taxa. During the middle Paleocene, palaechthonids dominated the plesiadapiform faunas of the Rocky Mountain corridor. As the climate deteriorated into the late Paleocene, plesiadapids began to dominate this fauna, and the few palaechthonids known were restricted, for the most part, to more southern paleogeographic regions. With the onset of the warming trend at the beginning of the Eocene, microsyopids appeared in northern faunas along with other taxa, such as rodents. At this time, plesiadapids slowly disappeared until, by the Clarkforkian-Wasatchian boundary, they were essentially gone. The following scenario can explain the above pattern.

Microsyopoids were subtropical forms, represented by palaechthonids in the middle Paleocene and distributed along the Rocky Mountain corridor. As the cooling in the later Paleocene developed, microsyopoids were restricted to more southerly geographic areas that were essentially unrepresented in the fossil record. During this time, plesiadapids (and other plesiadapiform families), which were a more temperate group, spread into many areas along the Rocky Mountain corridor. With the warming trend in the early Eocene, microsyopids (which had descended from palaechthonids during their restriction to southern latitudes) reappeared in northern localities. Plesiadapids disappeared because of the onset of subtropical climates along the Rocky Mountain corridor and also because of their inability to compete successfully with new immigrating groups, particularly rodents (Maas, Krause, and Strait, 1988).

Dental evidence and body size estimates support the last two conclusions. The emphasis on slicing incisors and shearing molars, combined with relatively small body sizes for most microsyopids, supports the conclusion that most of the species in this family were insectivorous. Some of the larger, later species (such as *Megadelphus lundeliusi*) have dental characteristics which suggest a more omnivorous diet. The dental attributes of microsyopids (emphasis on shearing, de-emphasis on crushing) and paromomyids (emphasis on crushing, puncturing and shearing concentrated in a single tooth, lower P4) differentiate both from adapids and omomyids and suggest that dietary differences

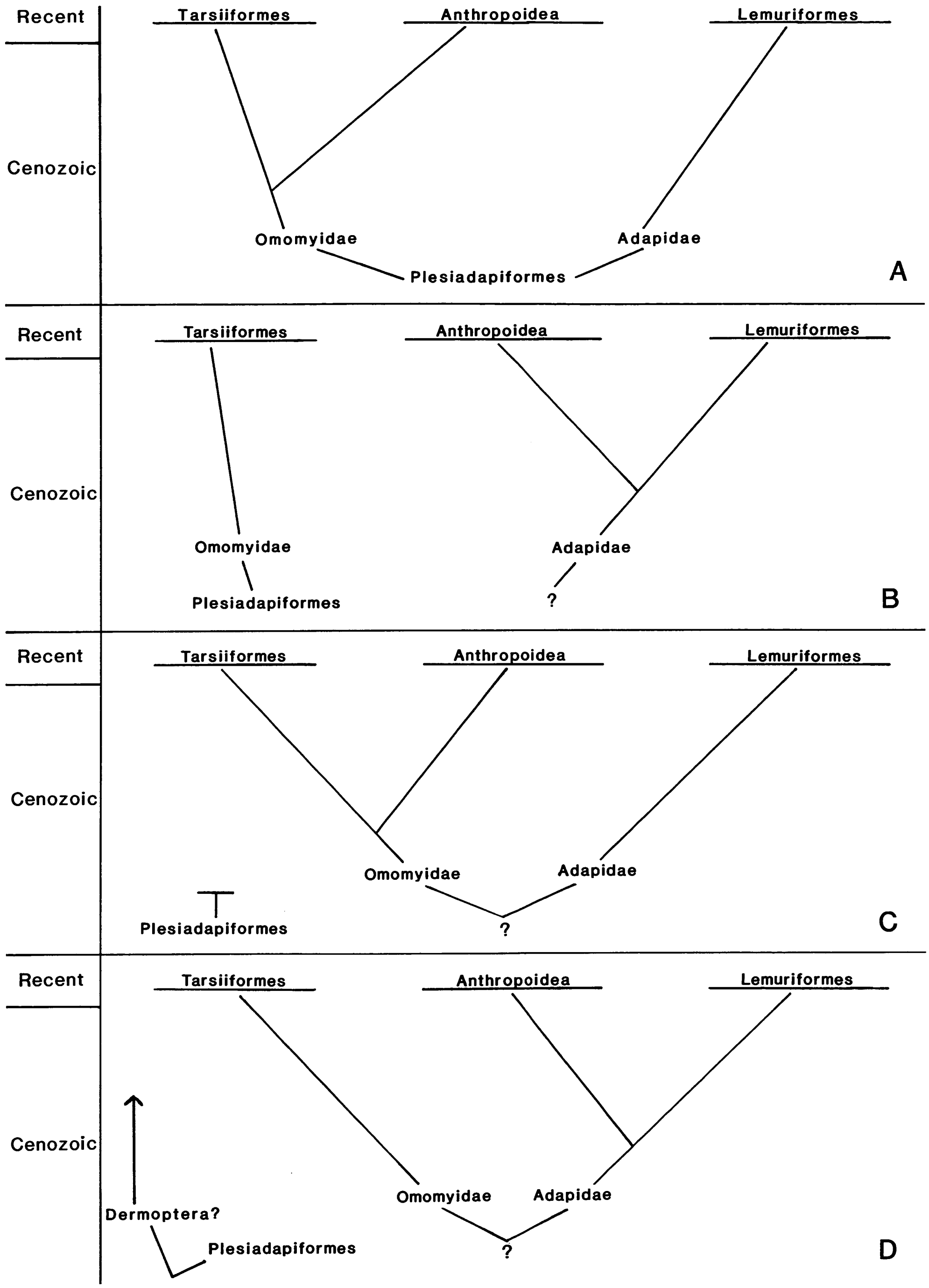

Figure 58. Schematic representation of four possible Plesiadapiformes-Primate relationships. A, represents a possible relationship between plesiadapiforms and euprimates; this is consistent with a plesiadapiform origin for euprimates. B, represents a possible relationship between plesiadapiforms and tarsiiforms; this is consistent with a Plesitarsiiformes-Simiolemuriformes dichotomy. C, Euprimates and plesiadapiforms not directly related; both may have originated from the same insectivore group or their origins may be polyphyletic. D, Plesiadapiforms and fossil dermopterans share common ancestry with one another, not directly related to euprimates. D is option favored in this report.

may have been at least partly responsible for the lack of apparent competition between adapids and omomyids and either of the other two families.

CLASSIFICATION

I have included Plesiadapiformes in Primates? as a suborder. Plesiadapiforms had reached an evolutionary grade comparable to that of the living tree shrews, not quite insectivore, yet not quite primate either (see Figure 58). Plesiadapiforms, in general, can be recognized by enlarged, lower central incisors (of various forms) and by general dental, cranial, and postcranial similarities (both primitive and convergent) with the earliest recognized primates of modern aspect.

Within Plesiadapiformes I recognize two superfamilies, Plesiadapoidea and Microsyopoidea.

CLASSIFICATION

Grandorder Archonta?
- Order Dermoptera?
    - *Remiculus*
    - *Plagiomene*
    - *Elpidophorus*
    - *Worlandia*
    - *Planetetherium*
- Order Insectivora?
    - Suborder Tupaiiformes
        - Tupaiidae
            - *Tupaia*
            - *Ptilocercus*
    - Suborder ?
        - Superfamily Apatemyoidea
            - Apatemyidae
                - *Apatemys*
                - *Unuchinia*
                - *Teilhardella*
                - *Labidolemur*
                - *Jepsenella*
                - *Sinclairella*
        - Superfamily Mixodectoidea
            - Mixodetidae
                - *Mixodectes*
                - *Dracontolestes*
            - Mixodectidae, *incertae sedis*
                - *Eudaemonema*
- Order Primates?
    - Superfamily ?
        - Pugatoriidae
            - *Purgatorius*
    - Superfamily Plesiadapoidea
        - Paromomyidae
            - Paromomyinae
                - *Paromomys*
            - Phenacolemurinae
                - *Phenacolemur*
                - *Ignacius*
                - *Elwynella*
        - Plesiadapidae
            - *Plesiadapis*
            - *Pronothodectes*
            - *Nannodectes*
            - *Chiromyoides*
            - *Platychoerops*
        - Carpolestidae
            - *Elphidotarsius*
            - *Carpodaptes*
            - *Carpolestes*
        - Saxonellidae
            - *Saxonella*
        - Picrodontidae
            - *Picrodus*
            - *Zanycteris*
    - Superfamily Microsyopoidea
        - Palaechthonidae
            - Palaechthoninae
                - *Palaechthon*
                - *Palenochtha*
                - *Premnoides*
            - Plesiolestinae
                - *Plesiolestes*
                - *Torrejonia*
        - Microsyopidae
            - Uintasoricinae
                - *Uintasorex*
                - *Niptomomys*
                - *Alveojunctus*
            - Navajoviinae
                - *Navajovius*
            - Navajoviinae?
                - *Berruvius*
            - Micromomyinae
                - *Micromomys*
                - *Tinimomys*
            - Microsyopinae
                - *Arctodontomys*
                - *Microsyops*
                - *Craseops*
                - *Megadelphus*

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APPENDIX I

Appendix I. Body size, shearing and crushing potentials for various plesiadapiforms and other primates. Arranged by family and Land-Mammal Age, Torrejonian through Uintan. See text for discussion of derivation of shearing and crushing potential estimates.

Land Mammal Age	Taxon	Estimated Body Weight (grams)	Estimated Shearing Potential	Estimated Crushing Potential
	Family Plesiadapidae			
Torrejonian	*Pronothodectes matthewi*	308	1.66	.49
	Pronothodectes jepi	408	1.35	.40
	Family Palaechthonidae			
	Plesiolestes problematicus	308	1.57	.33
	Plesiolestes nacimienti	275	1.87	.53
	Palaechthon alticuspis	150	1.74	.41
	Family Plesiadapidae			
Tiffanian	*Nannodectes gidleyi*	740	1.52	.40
	Nannodectes simpsoni	625	1.71	.42
	Plesiadapis rex	930	1.49	.41
	Palaechthonidae			
	Torrejonia sirokyi	1335	1.62	.38
	Family Carpolestidae			
	Carpodaptes hazelae	104	1.52	.35
	Family Plesiadapidae			
Clarkforkian	*Plesiadapis dubius*	727	1.51	.41
	Plesiadapis cookei	4147	1.53	.48
	Family Paromomyidae			
	Phenacolemur praecox	480	1.74	.53
	Family Microsyopidae			
	Arctodontomys simplicidens	720	1.66	.35
	Family Carpolestidae			
	Carpolestes nigridens	140	1.43	.34
	Family Microsyopidae			
Wasatchian	*Arctodontomys wilsoni*	485	1.71	.38
	Microsyops latidens	672	1.71	.46
	Niptomomys doreenae	60	1.72	.42
	Tinimomys graybullensis	35	1.58	.43
	Paromomyidae			
	Phenacolemur praecox	437	1.52	.46
	Ignacius graybullianus	260	1.62	.54
	Family Adapidae			
	Cantius mckennai	1644	1.49	.47
	Family Omomyidae			
	Teilhardina tenuicula	180	1.51	.40
	Tetonius matthewi	283	1.57	.49
	Absarokius abbotti	237	1.50	.42
	Loveina zephyri	174	1.50	.42
	Shoshonius cooperi	192	1.52	.38
	Family Microsyopidae			
Bridgerian	*Microsyops elegans*	1090	1.61	.38
	Family Adapidae			
	Notharctus robinsoni	4658	1.47	.43
	Family Omomyidae			
	Omomys carteri	403	1.69	.44
	Trogolemur myodes	150	1.74	.50
	Hemiacodon gracilis	1300	1.51	.44
	Family Microsyopidae			
Uintan	*Microsyops kratos*	3483	1.68	.46
	Craseops sylvestris	6390	1.66	.40
	Uintasorex parvulus	32	1.90	.39
	Family Adapidae			
	Mahgarita stevensi	997	1.39	.43
	Family Omomyidae			
	Macrotarsius montanus	2014	1.77	.41
	Ourayia uintensis	2281	1.56	.46

APPENDIX II

Appendix II. Body Weight Estimates (Ln of grams) and Confidence Intervals (95%) for various plesiadapiform and other primate species. Arranged by Land-Mammal Age, Torrejonian through Uintan. N sample size.

Taxon(N)	Estimated Body Confidence Weight	Intervals
Torrejonian		
Pronothodectes matthewi(9)	5.73	5.56–5.90
Pronothodectes jepi(11)	6.01	5.86–6.16
Torrejonia wilsoni(2)	6.84	6.73–6.95
Palaechthon woodi(2)	4.72	4.50–4.94
Plesiolestes problematicus(30)	5.73	5.56–5.90
Elphidotarsius florencae(14)	4.74	4.50–4.98
Plesiolestes nacimienti(1)	5.61	5.44–5.78
Palaechthon alticuspis(10)	5.01	4.70–5.22
Tiffanian		
Carpodaptes hazelae(53)	4.64	4.44–4.88
Carpolestes dubius(23)	5.25	5.04–5.44
Micromomys vossae(1)	3.40	3.00–3.66
Torrejonia sirokyi(3)	7.20	7.11–7.29
Ignacius frugivorus(4)	5.18	4.99–5.37
Chiromyoides minor(1)	5.54	5.37–5.70
Navajovius kohlhaasae(1)	4.41	4.17–4.65
Nannodectes intermedius(49)	6.07	5.91–6.21
Nannodectes gazini(22)	5.92	5.75–6.09
Nannodectes simpsoni(11)	6.44	6.31–6.57
Nannodectes gidleyi(12)	6.61	6.49–6.73
Plesiadapis anceps(11)	6.67	6.55–6.80
Plesiadapis rex(129)	6.84	6.72–6.94
Plesiadapis churchilli(4)	7.17	7.07–7.27
Plesiadapis fodinatus(57)	6.89	6.77–6.99
Clarkforkian		
Plesiadapis dubius(10)	6.59	6.47–6.71
Arctodontomys simplicidens(2)	6.58	6.46–6.70
Niptomomys doreenae(15)	4.48	4.37–4.61
Plesiadapis gingerichi(3)	7.94	7.87–8.01
Plesiadapis cookei(15)	8.33	8.26–8.40
Phenacolemur praecox(11)	6.17	6.04–6.32
Carpolestes nigridens(15)	4.94	4.70–5.14
Ignacius graybullianus(3)	6.09	5.94–6.23
Phenacolemur pagei(9)	5.89	5.73–6.05
Wasatchian		
Arctodontomys wilsoni(16)	6.18	6.04–6.32
Phenacolemur simonsi(8)	4.77	4.55–4.99
Niptomomys doreenae(32)	4.09	3.81–4.38
Phenacolemur praecox(21)	6.08	5.93–6.23
Tinimomoys graybullensis(7)	3.56	3.30–3.85
Teilhardina tenuicula(9)	5.19	5.01–5.39
Ignacius graybullianus(4)	5.56	5.39–5.74
Teilhardina americana(1)	5.11	4.91–5.32
Tetonius matthewi(11)	5.65	5.48–5.81
Cantius ralstoni(16)	7.19	7.10–7.28
Cantius mckennai(15)	7.40	7.32–7.50
Cantius abditus(1)	8.09	8.02–8.16
"Copelemur" feretutus(2)	7.56	7.48–7.64
"Copelemur" consortutus(5)	7.38	7.32–7.44
Copelemur tutus(1)	8.19	8.14–8.24
Microsyops latidens(28)	6.51	6.42–6.60
Bridgerian		
Omomys carteri(2)	6.00	5.85–6.15
Hemiacodon gracilis(3)	7.17	7.07–7.27
Washakius insignis(3)	5.72	5.54–5.89
Utahia kayi(1)	5.28	5.09–5.47
Anaptomorphus wortmani(4)	5.67	5.50–5.84
Trogolemur myodes(1)	5.01	4.82–5.19
Uintanius ameghini(2)	5.27	5.08–5.46
Aycrossia lovei(2)	5.76	5.60–5.78
Microsyops elegans(18)	6.99	6.89–7.09
Microsyops annectens(6)	7.66	7.58–7.74
Smilodectes mcgrewi(2)	7.95	7.88–8.02
Notharctus robinsoni(2)	8.45	8.38–8.52
Elwynella oreas(2)	5.82	5.75–5.98
Uintan		
Mahgarita stevensi(1)	6.90	6.79–7.01
Microsyops kratos(1)	8.16	8.08–8.22
Craseops sylvestris(1)	8.76	8.67–8.85
Macrotarsius montanus(3)	7.62	7.52–7.72
Ourayia uintensis(1)	7.73	7.65–7.81
Uintasorex parvulus(3)	3.47	3.18–3.81
Trogolemur myodes(2)	4.09	3.85–4.38
Chumasius balchi(2)	5.87	5.70–6.03
Dyseolemur pacificus(2)	5.68	5.50–5.86
Stockia powayensis(1)	6.31	6.16–6.45
Rooneyia viejaensis(1)	7.51	7.40–7.62