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ERRATA

Page 57, line 4, "late early" should read "early middle."

SYSTEMATICS OF EARLY EOCENE MICROSYOPINAE (MAMMALIA, PRIMATES) IN THE CLARK'S FORK BASIN, WYOMING

By

Gregg F. Gunnell

Abstract.—Two genera and five species of microsyopine Microsyopidae are known from middle Clarkforkian through middle Wasatchian age strata in the Clark's Fork Basin, Wyoming. *Arctodontomys* (n. gen.) and *Microsyops* are among the few archaic plesiadapiform primates to survive well into the Eocene. Species represented in the early Eocene of the Clark's Fork Basin include: *Arctodontomys simplicidens* (Rose), middle through late Clarkforkian, *Arctodontomys wilsoni* (Szalay), early Wasatchian, *Arctodontomys nuptus* (Cope), early middle Wasatchian, *Microsyops angustidens* (Matthew), middle Wasatchian, and *Microsyops* sp. A, late middle Wasatchian. *Cynodontomys alfi* is here regarded as a synonym of *Microsyops angustidens*.

INTRODUCTION

The primate family Microsyopidae is one of only two families of archaic plesiadapiform primates to survive and flourish through the early Eocene of the North American Western Interior. At the beginning of the Eocene (middle to late Clarkforkian Land-Mammal Age, see Rose, 1981), four families of archaic primates were still present: Plesiadapidae, Carpolestidae, Paromomyidae, and Microsyopidae. However, at the boundary between the Clarkforkian and Wasatchian land-mammal ages, the former two families disappeared (Rose and Bown, 1982, note the possible survival of one lineage of *Plesiadapis* into the Wasatchian). The latter two families, Microsyopidae and Paromomyidae, survived well into the Eocene, and representatives of each are known from the Uintan Land-Mammal Age (middle or late Eocene) in North America (Simpson, 1955; Szalay, 1969).

North American Eocene Microsyopidae are represented by evolutionary radiations at two distinct body sizes, one diminutive and the other larger. The radiation of small taxa is represented by five genera, three assigned to the subfamily Uintasoricinae (*Niptomomys*, *Uintasorex*, and *Alveojunctus*; see Bown, 1982), and two of uncertain placement within Microsyopidae (*Micromomys* and *Tinimomys*; see Gunnell and Gingerich, 1981). Larger microsyopids, placed in the subfamily Microsyopinae, include three Eocene genera: *Arctodontomys* (new genus), *Microsyops*, and *Craseops*. *Arctodontomys* is known from the earliest Eocene, spanning the middle Clarkforkian through early Wasatchian Land-Mammal Ages. *Microsyops*, the most common of microsyopines, is present from the middle Wasatchian through Uintan Land-Mammal Ages (Stock, 1938; Szalay, 1969). *Craseops* is known only from the Uintan Land-Mammal Age (Stock, 1934).

The radiation of early Eocene Microsyopinae is discussed in this paper, focusing on evidence from a northern extension of the Bighorn Basin, specifically, the Clark's Fork Basin in Park County, Wyoming. In recent years, field parties from the University of Michigan have collected some 130 new microsyopine specimens, most of which come from tightly controlled stratigraphic sections. New evidence on the species-level evolution of microsyopine primates is presented in the following discussion.

The stratigraphic setting and temporal succession of Clark's Fork Basin faunas are discussed in Gingerich et al. (1980), Rose (1981), and Gingerich (1982, 1983). Zones of the Wasatchian Land-Mammal Age employed here are those developed by Granger (1914) and Schankler (1980), as reviewed in Gingerich (1983). "Sandcouleean" (Wa_1-Wa_2) is equivalent to early Wasatchian, "Graybullian" (Wa_3-Wa_5) is equivalent to middle Wasatchian, and "Lysitean" (Wa_6) and "Lostcabinian" (Wa_7) are together equivalent to late Wasatchian. Dental and other anatomical nomenclature employed in this paper follows Szalay (1969).

Fossil localities prefaced by SC are University of Michigan localities in the Sand Coulee area of the Clark's Fork Basin. Localities prefaced by YM are Yale-Michigan localities in the central Bighorn Basin. The following museum acronyms are used in the text and figures: AMNH, American Museum of Natural History (New York); KU, Kansas University, Museum of Natural History (Lawrence); PU, Princeton University, Museum of Natural History (Princeton); UM, University of Michigan, Museum of Paleontology (Ann Arbor); USGS, United States Geological Survey (Denver); UW, University of Wyoming, Geology Museum (Laramie); YPM, Yale Peabody Museum (New Haven).

SYSTEMATIC PALEONTOLOGY

Order Primates Linnaeus, 1758
Infraorder 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.—North America: *Palaechthon* Gidley, 1923 (=*Talpohenach* Kay and Cartmill, 1977); *Plesiolestes* Jepsen, 1930; *Palenochtha* Simpson, 1935; *Torrejonia* Gazin, 1968; *Navajovius* Matthew and Granger, 1921; *Arctodontomys,* new genus; *Microsyops* Leidy, 1872; and *Craseops* Stock, 1934. Table 1 lists the five species of Microsyopinae recognized as valid in the Clark's Fork Basin.

Arctodontomys n. gen.

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

Type species.—Arctodontomys simplicidens (Rose, 1981).

Included species.—Arctodontomys simplicidens (Rose, 1981), *Arctodontomys wilsoni* (Szalay, 1969), and *Arctodontomys nuptus* (Cope, 1881).

Age and Distribution.—Early Eocene, early middle Clarkforkian through middle Wasatchian of North America.

Diagnosis.—Differs from *Microsyops* in lacking a metaconid on P_4, in having a weakly developed talonid basin on P_4, in lacking mesostyles on upper molars, in having a weak to absent metacone on P^4, and in having more acute, less bulbous cusps, especially on molars.

Etymology.—From *arktos*, Gr., bear; *odontos*, Gr., tooth; *mys*, Gr., mouse; in reference to the Beartooth Mountains bordering the Clark's Fork Basin on the west, and the beartooth-like, pointed, projecting, lower incisor typical of the family.

Arctodontomys simplicidens (Rose, 1981)
Fig. 1

Microsyops simplicidens Rose, 1981, p. 52, fig. 20.

Holotype.—UM 67214, right mandible with P_2-P_4, and associated M_1, from UM locality SC-137, Clark's Fork Basin, Wyoming.

Age and Distribution.—Earliest Eocene, early middle through late Clarkforkian, known only from the Clark's Fork Basin at present.

Diagnosis.—Differs from the other *Arctodontomys* species in having simple P_4 structure. P_4 with no evidence of a paraconid or metaconid; P_4 talonid with a single central cusp and little or no basin development. Also differs in having P_2 larger than P_3. *A. simplicidens* is slightly larger than *A. wilsoni* and smaller than *A. nuptus.*

Discussion.—*A. simplicidens* has been adequately described by Rose (1981) and little can be added here. Measurements of the Clark's Fork Basin sample of *Arctodontomys simplicidens* are summarized in Table 2.

Hypodigm.—UM localities and specimen numbers from the Clark's Fork Basin: SC-10—69360 (L Max M^1); SC-74—66178 (R Mand P_4-M_2); SC-137—67214 (R Mand P_{2-4}, M_1) holotype; SC-143—68287 (R Mand M_3), 75454 (L I_1), 83015 (L M_x), and 83019 (R M_1). From middle Clarkforkian strata in the Foster Gulch area, northern Bighorn Basin, UM locality FG-6—74128 (R M_1).

Additional Clarkforkian *A. simplicidens* specimens include PU 23552, and PU 23553, from SC-143.

Arctodontomys wilsoni (Szalay, 1969)
Fig. 2

Microsyops wilsoni Szalay, 1969, p. 249, fig. 9-13; Pl. 30, fig. 1-7; Pl. 32, fig. 1-8. Bown and Rose, 1976, p. 122. Bown, 1979, p. 67, fig. 44b-e.

Holotype.—KU 8520, left mandible with P_4-M_2, collected from lower Graybullian beds, Willwood Formation. Holotype was collected at KU locality 32 (SW1/4, Section 28, T50N, R93W) on the south fork of Elk Creek, Big Horn County, Wyoming.

Age and Distribution.—Early Eocene, early Wasatchian Land-Mammal Age of Bighorn Basin, Wyoming and Four Mile area, Colorado.

Diagnosis.—Differs from *A. simplicidens* in being significantly smaller and in having a more complex P_4, with small paraconid or enamel fold and a distinct talonid basin, although the hypoconid and entoconid may not be distinct. Differs from *A. nuptus* in being significantly smaller and in having less well-developed hypoconulids on lower molars.

Description.—*A. wilsoni* is the most common species of *Arctodontomys*. It has been

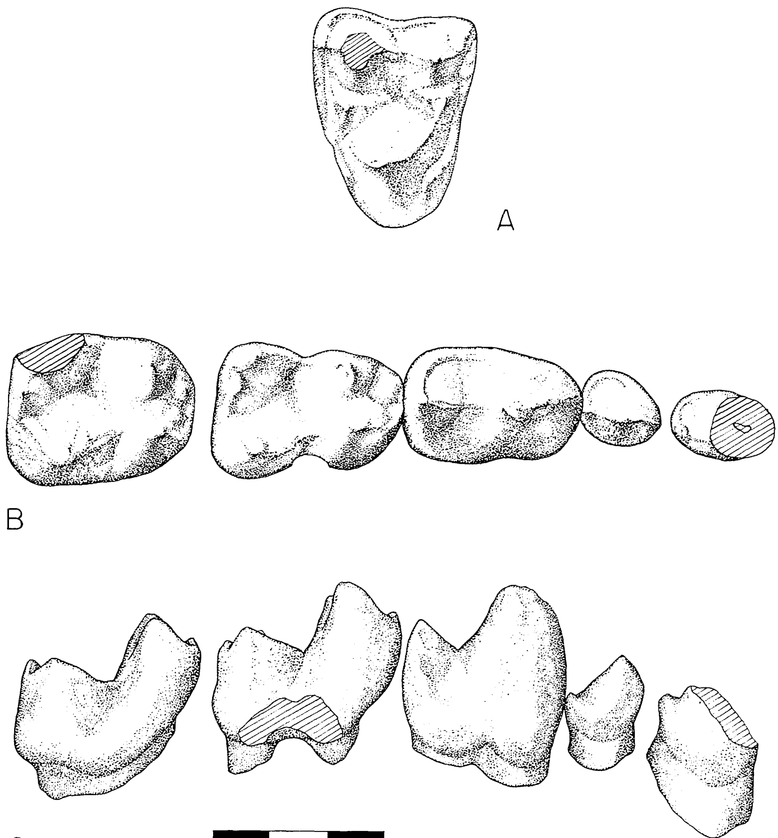


FIG. 1— Upper and lower dentition of middle Clarkforkian *Arctodontomys simplicidens* (Rose). A, left M^1 (UM 69360) from UM locality SC-10, in occlusal view. B, right composite dentition (based on UM 67214, holotype, from UM locality SC-137, right P_2-P_4, M_1, and UM 66178, right P_4-M_2 from UM locality SC-74) in oclusal view. C, same in lateral view (Figures B and C from Rose, 1981).

adequately described by Szalay (1969), Bown and Rose (1976) and Bown (1979). However, certain aspects of its morphology deserve greater attention.

The morphology of P^3 and $P_{2\text{-}3}$, not well-known previously, can now be described. P^3 is a simple tooth, smaller than P^4. It is dominated by a single cusp (paracone?), sometimes with a small posterior stylar cusp. It is triangular in occlusal outline, and three-rooted. P_2 is a small tooth with a single major cusp (protoconid). It has a very small talonid at the base of this cusp and is single-rooted. P_2 is separated from I_1 and from P_3 by small diastemata, but there is no

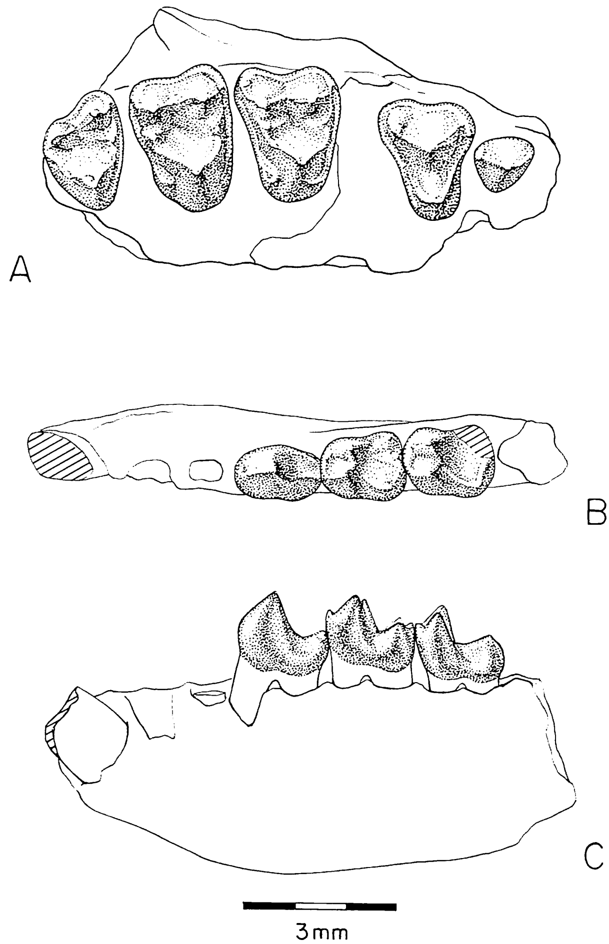


FIG. 2— Upper and lower dentition of early Wasatchian *Arctodontomys wilsoni* (Szalay). A, right maxilla (UM 71262) with P^3-M^3, from UM locality SC-2, in occlusal view. B, left mandible with P_4-M_2 (UM 68321) from UM locality SC-2, in occlusal view. C, same in lateral view.

indication of either P_1 or a canine. P_3 is very similar to P_2. It is of the same height and is only slightly more robust. It, too, has only a protoconid, but the talonid is better developed than in P_2, sometimes possessing a small centrally-located cusp. P_3 may be either single or double-rooted, but normally possesses only a single root. Measurements of the Clark's Fork Basin sample of *Arctodontomys wilsoni* are summarized in Table 3.

Discussion.—Bown and Gingerich (1973) and Bown and Rose (1976) correctly point out that the P^4 attributed by Szalay (1969) to *A. wilsoni* is, in fact, a specimen representing *Tetonius*, an omomyid primate. Bown and Rose also note that P^4 of *A. wilsoni* has a moderate to well developed metacone. Larger samples now available indicate that metacone development is rather variable and that in many cases no metacone is present on P^4.. P_3 was described as being two-rooted (Bown and Rose, 1976), however, in the sixteen specimens now known that preserve either P_3 or its roots, only one P_3 is clearly two-rooted. Three others have a single root that branches into two roots at or slightly below the mandibular margin. Bown and Rose (1976) also stated that P_4 of *A. wilsoni* has a well developed talonid basin with distinct hypoconid and entoconid cusps. This feature is also quite variable. Most specimens have a well-developed hypoconid. An entoconid may or may not be present, and in the majority of cases is absent.

Hypodigm.—UM localities and specimen numbers from the Clark's Fork Basin: SC-2—67504 (RM_2), 67667 (R Mand P_4-M_1), 68321 (L Mand P_4-M_2), 68598 (L Mand P_4-M_2), 71262 (R Max P^3-M^3), 71285 (L Max M^{1-2}), 71286 (L Max P^4-M^2), 78936 (R Max P^4-M^3); SC-4—72866 (L M_{1-2}); SC-6—64855 (R Mand M_{1-2}); SC-12—64809 (L Mand M_{2-3}), 64817 (L Mand M_2); SC-14—64878 (R Mand P_4-M_2); SC-16—75346 (LI^1); SC-26—65192 (L Mand M_{1-2}); SC-27—80785 (R Max P^{3-4}, M^{1-2}); SC-38—75591 (L Max P^4-M^3); SC-40—80433 (R Mand P_4); SC-42—65443 (LP_4); SC-47—74122 (L Mand M_{1-2}); SC-54—65687 (R Mand edent.), 65691 (RM^x); SC-96—66463 (L Mand M_{2-3}); SC-133—67148 (L Mand P_4-M_2), 68106 (LI^1), 68459 (L Mand M_1), 82720 (L Mand M_{1-3}), 82732 (R Mand M_{2-3}); SC-151—67440 (L Mand M_2); SC-159—71022 (RI_1); SC-160—68139 (R Mand M_{1-3}), 77417 (LM_2); SC-161—77478 (L Max M^{1-3}), 80682 (L Mand M_{1-2}), 82279 (LM_2), 82288 (R P_4-M_1); SC-192—69130 (RI^1); SC-207—69455 (R Mand M_{1-2}); SC-210—75808 (LI^1); SC-211—69727 (R Mand M_{1-2}), 69738 (R Max P^4-M^2); SC-213—69810 (L Mand P_{3-4}), 82144 (L Mand P_4-M_1); SC-311—76617 (L Mand M_{1-2}); SC-323—79364 (R Max M^{1-3}). Early Wasatchian from the Foster Gulch area northern Bighorn Basin: FG-18—75857 (L Mand M_{1-3}), 75877 (R Max P^4-M^2); FG-25—76252 (LM_1).

Additional early Wasatchian *A. wilsoni* specimens from the Bighorn Basin include the following: KU 8520 (L Mand P_4-M_2, holotype); PU 18028 (L Mand P_4-M_2); USGS 9209 (L Mand P_4-M_1); UW numbers 6905 (L Max P^4-M^2), 7154 (R Max M^{1-3}), 7172 (L Mand P_3-M_2), 7173 (R Mand M_{1-2}), 7194 (L Mand P_4-M_3), 7195 (R Mand P_4-M_2, L Mand M_{1-3}), 8800 (R Max P^{2-4}), 8822 (L Mand P_4), 8834 (L Mand P_4-M_1), 8918 (L Mand P_4-M_2); YPM numbers 30842 (L Mand P_4), 30843 (R Mand P_4-M_1), 30846 (L Max P^4-M^2), 30848 (L Mand P_4), 30849 (L Mand P_{3-4}), 30853 (L Mand M_{1-2}), 30854 (RP_4), 30857 (L Mand P_4), 30859 (L Mand P_4), 30981 (L Mand P_4-M_1), 31378 (L Mand M_2), 34533 (LM_1), and others.

Arctodontomys nuptus (Cope, 1882)
Fig. 3

Pantolestes nuptus Cope, 1882, p. 150; 1884, p. 720, Pl. 24e, fig. 7-7a.
Diacodexis nuptus, Gazin, 1952, p. 71.
Microsyops angustidens (in part), Szalay, 1969, p. 256.

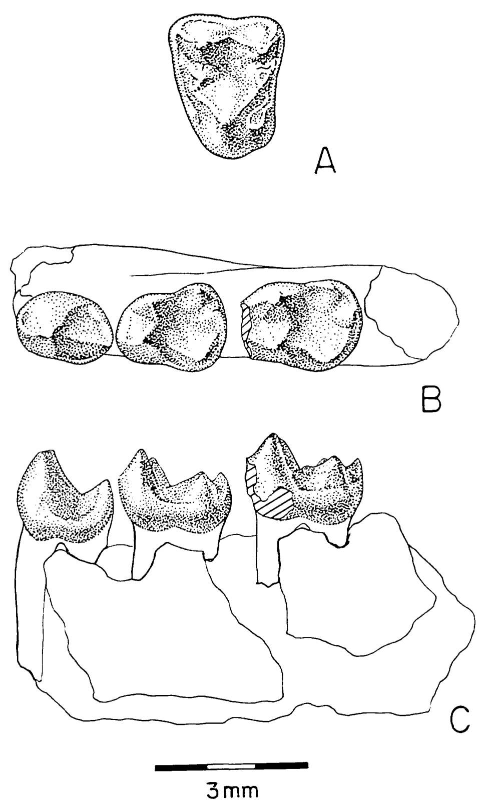


FIG. 3— Upper and lower dentition of early middle Wasatchian *Arctodontomys nuptus* (Cope). A, left upper M^2 (UM 82041) from UM locality SC-112, in occlusal view. B, left mandible, P_4-M_2 (UM 66787) from UM locality SC-111, in occlusal view. C, same in lateral view.

Holotype.—AMNH 4699, right mandible with P_4-M_2, from the "*Coryphodon* beds," Wasatch Formation, Bighorn Basin, Wyoming. This locality is probably near Dorsey Creek, southwest of the settlement of Otto, Wyoming (see Gingerich, 1980).

Age and Distribution.—Early Eocene, late early Wasatchian, from the Bighorn and Clark's Fork Basins, Wyoming.

Diagnosis.—Differs from *A. wilsoni* in being significantly larger, and in having better developed hypoconulids on lower molars. Differs from *A. simplicidens* in being slightly larger, in having a more complex P_4, and in having better developed hypoconulids on lower molars.

Description.—P_4 of *A. nuptus* has a large protoconid, a distinct paraconid, and no metaconid. The talonid is quite well developed with a large hypoconid and small entoconid. It has a well developed buccal cingulid.

The lower first molar has a distinct protoconid and a paraconid and metaconid of equal height. The paraconid is separated from the metaconid and is centro-buccally placed, more buccally than is seen in *A. wilsoni.* It has a well-developed paracristid. M_1 in *A. nuptus* has a large, deep talonid basin with hypoconid, entoconid and hypoconulid well developed. The hypoconulid is appressed to the entoconid and it is better developed than in the other two species of the genus. The oblique cristid joins the trigonid more buccally than in *A. wilsoni,* but shares this feature with *A. simplicidens.* There is a distinct buccal cingulid on M_1.

The second lower molar is similar to the first in most respects. The only clear distinction between the two is in the position of the paraconid. It is nearer the lingual side of the tooth and closely appressed to the metaconid on M_2. The paraconid is often barely recognizable in worn teeth. As a consequence of the position of the paraconid, the paracristid is more extended bucco-lingually than in M_1. M_2 also has a relatively strong buccal cingulid.

The third lower molar trigonid is compressed anterior-posteriorly with the paraconid closely appressed to the metaconid which is often not distinct from this cusp. A strong paracristid is developed as in M_2. M_3 has a large hypoconulid positioned posterior to the entoconid, thus extending the talonid. In other respects M_3 is similar to the other molars. The second molar is larger in both length and width than the first molar, while the third molar is usually the longest, but also the least wide. None of the lower molars has a mesoconid.

The upper dentition is not well known, however some isolated and broken molars can be identified as *A. nuptus.* They are similar in most respects to those of *A. wilsoni,* except that they are larger. The first and second upper molars have distinct protocones, paracones, and metacones, the latter two cusps being of equal height. There is a small, but distinct hypocone on a talon slightly better developed than in *A. wilsoni.* M^{1-2} possess distinct paraconules and metaconules, with the paraconules better developed than the metaconules. Metaconules on M^{1-2} of *A. nuptus* are stronger than those seen in *A. wilsoni.* Small parastyles and metastyles are present, as well as a precingulum and a buccal cingulum. There is no mesostyle.

The upper third molar is smaller than the other two upper molars. It has a reduced metacone, more widely separated from the paracone than in M^{1-2}. The metaconule is often absent and always reduced, when present. The hypocone is small with little talon development. The stylar shelf is reduced and there are no stylar cusps. Measurements of the Clark's Fork Basin sample of *Arctodontomys nuptus* are summarized in Table 4.

Discussion.—As Szalay (1969) noted, *A. nuptus* is quite similar to *Microsyops angustidens.* He believed that the differences in P_4 morphology were due to intraspecific or individual variation and chose not to separate the two forms specifically. Further work has shown that the lack of a P_4 metaconid (see discussion section below) is a consistent character that separates the early Wasatchian microsyopines from the middle and late Wasatchian forms. I think that this character, in conjunction with other features, is sufficient to ally *A. nuptus* with earlier *Arctodontomys* and to distinguish it from later *Microsyops.* Lack of a P_4 metaconid and the lack of a mesostyle on upper molars are the two most consistent distinguishing characteristics of *Arctodontomys.* Although upper molars of *A. nuptus* are not well known, the few specimens available show no sign of a mesostyle.

The principle characteristic distinguishing *A. nuptus* and *A. wilsoni* is size. Measurements of the lower first molar were taken on five *A. nuptus* specimens and on ten *A. wilsoni* specimens. Lower first or second molar area can be used to estimate body weight in mammals (see Gingerich and Ryan, 1979; Gingerich, Smith and Rosenberg, 1982). Mean M_1 area for *A. nuptus* as a natural log is 2.17. The mean area for *A. wilsoni* is 1.79. Observed ranges of these measurements do not overlap (see Fig. 6). Subjecting these samples to a two-tailed Student's t-test, testing the hypothesis that both samples came from a single population of similar sized animals, this hypothesis is rejected at the 95% level. This distinction in size clearly warrants separation of the two samples into distinct species.

"*Pantolestes*" *nuptus* Cope is conspecific with large *Arctodontomys* specimens from the Clark's Fork Basin: the species name *nuptus* is available and appropriately applied to these specimens. No other name has been proposed for large microsyopines lacking a metaconid on P_4.

Hypodigm.—UM localities and specimen numbers from the Clark's Fork Basin: SC-64—66654 (RM_1), 82040 (LM_1, M_3); SC-111—66780 (L Mand M_{2-3}), 66787 (L Mand P_4-M_2); SC-112—66798 (LM_2), 79907 (RM_1), 79917 (R Mand M_{1-2}), 82041 (LM^2); SC-254—73055 (LM_1); SC-325—79482 (LM_1), 79486 (L Max M^{2-3}, L Mand M_{2-3}).

Additional early middle Wasatchian Bighorn Basin specimens representing *A. nuptus* include: AMNH 4699 (R Mand P_4-M_2, holotype); USGS numbers 3713 (LM_1), 3781 (L Mand M_{1-2}), 3792 (R Mand M_{1-2}), 3812 (L Mand P_4-M_2), 3818 (R Mand M_{1-2}), 6027 (R Mand M_{1-2}), 7939 (RM_1); YPM numbers 24995 (LM_1), 26014 (R Mand M_{1-2}), and 30818 (RM_2).

Microsyops Leidy, 1872

Limnotherium (in part), Marsh, 1871, p. 43.
Microsyops Leidy, 1872, p. 363; Matthew, 1915, p. 468; Stock, 1938, p. 290; Robinson, 1966, p. 41; Gazin, 1976, p. 8; Bown, 1982, p. A47; Lucas, 1982, p. 19.
Bathrodon Marsh, 1872, p. 211.
Mesacodon Marsh, 1872, p. 212.
Palaeacodon Leidy, 1872, p. 356.
Microsyops (in part), Cope, 1881, p. 188; Szalay, 1969, p. 248.
Cynodontomys Cope, 1882, p. 188; Gazin, 1952, p. 20; White, 1952, p. 191; Kelly and Wood, 1954, p. 339; McKenna, 1960, 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.—*Microsyops elegans* (Marsh, 1871), *Microsyops annectens* (Marsh, 1872), *Microsyops scottianus* Cope, 1881, *Microsyops latidens* (Cope, 1882), *Microsyops angustidens* (Matthew, 1915), *Microsyops kratos* Stock, 1938, *Microsyops lundeliusi* (White, 1952), *Microsyops* sp. A (this paper).

Age and Distribution.—Early Eocene, middle Wasatchian through late Eocene, Uintan 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 cusps on molars.

Microsyops angustidens (Matthew, 1915)
Fig. 4

Cynodontomys angustidens Matthew, 1915, p. 477, fig. 47-48.
Cynodontomys alfi McKenna, 1960, p. 79, fig. 40.
Microsyops angustidens (in part), Szalay, 1969, p. 255, fig. 9-11; Pl. 35, fig. 3-6; Pl. 39, fig. 5-6.

Holotype.—AMNH 15073, left mandible with P_3-M_3, right mandible with P_4-M_2, from Graybullian beds, Wasatch Formation, Bighorn Basin, south of Otto, Wyoming.

Age and Distribution.—Early Eocene, middle Wasatchian from various localities in Wyoming, North Dakota, and Colorado.

Emended Diagnosis.—Differs from *M. latidens* by having less complex upper and lower fourth premolars. P_4 lacks a hypoconulid. As in all species of *Microsyops*, *M. angustidens* possesses a mesostyle, although mesostyle development is variable in this species.

Description.—Szalay (1969) has adequately described most of the dentition of *M. angustidens.* To his description can now be added descriptions of I_1, P_2 and M^3.

The lower central incisor is of a typical microsyopid form. It is lanceolate in shape with a recurved lower margin tapering to a point. The upper margin forms a long slicing blade that bulges bucco-dorsally before tapering to the tip. On an unworn tooth, a beaded row of enamel cuspules runs the length of the upper margin, but it is quickly lost with wear. P_2 is equal in height to P_3, but it is less complex than the latter tooth. It has a single cusp and little talonid development. P_2 is single rooted. There is a diastema separating P_2 from I_1, but no sign of a P_1 or a canine. M^3 is less reduced than its counterpart in *Arctodontomys.* It has a well-developed protocone, paracone, and metacone, all of equal height. There is a well-developed paraconule and a smaller metaconule. A small hypocone is present on a moderate talon. There is a distinct precingulum and a consistent buccal cingulum. A small, but distinct mesostyle or stylar shelf cuspule is usually present. Measurements of the Clark's Fork Basin sample of *Microsyops angustidens* are summarized in Table 5.

Discussion.—In his diagnosis, Szalay (1969) states that *M. angustidens* differs from *M. latidens* in lacking a mesostyle. Szalay's study was limited in that he had only two specimens available preserving upper teeth. It is now evident from more extensive collections that *M. angustidens* is rather variable in this regard and often does possess a mesostyle. Specimens in the UM and YPM collections show this characteristic. Admittedly, this is a variable character: some specimens show no mesostyle, others have only a cuspule on the stylar shelf, while still others have a true mesostyle. There is also varation as to which molars develop a mesostyle. Some specimens have a mesostyle on M^1 but not on the other molars, while others have mesostyles on M^{2-3} and lack it on M^1. Two possibilities suggest themselves. Either mesostyle development is highly variable, and as such, is of little taxonomic value, or *M. angustidens* represents an intermediate species in the process of adding a mesostyle. Since the species immediately preceding it consistently lacks a mesostyle and the species following it consistently possesses one, evidence seems to favor the latter possibility. A mesostyle, even if variably present, together with consistent development of a metaconid on P_4, is strong evidence to ally *M. angustidens* with *Microsyops* and distinguishing it from *Arctodontomys.*

Cynodontomys alfi was described by McKenna (1960). He maintained its distinction from *Microsyops angustidens* because of the primitive nature of its upper fourth premolar. This tooth is compressed antero-posteriorly and has a metacone that is very small or absent. Further study of McKenna's specimens indicates that this premolar does not belong with the upper molar

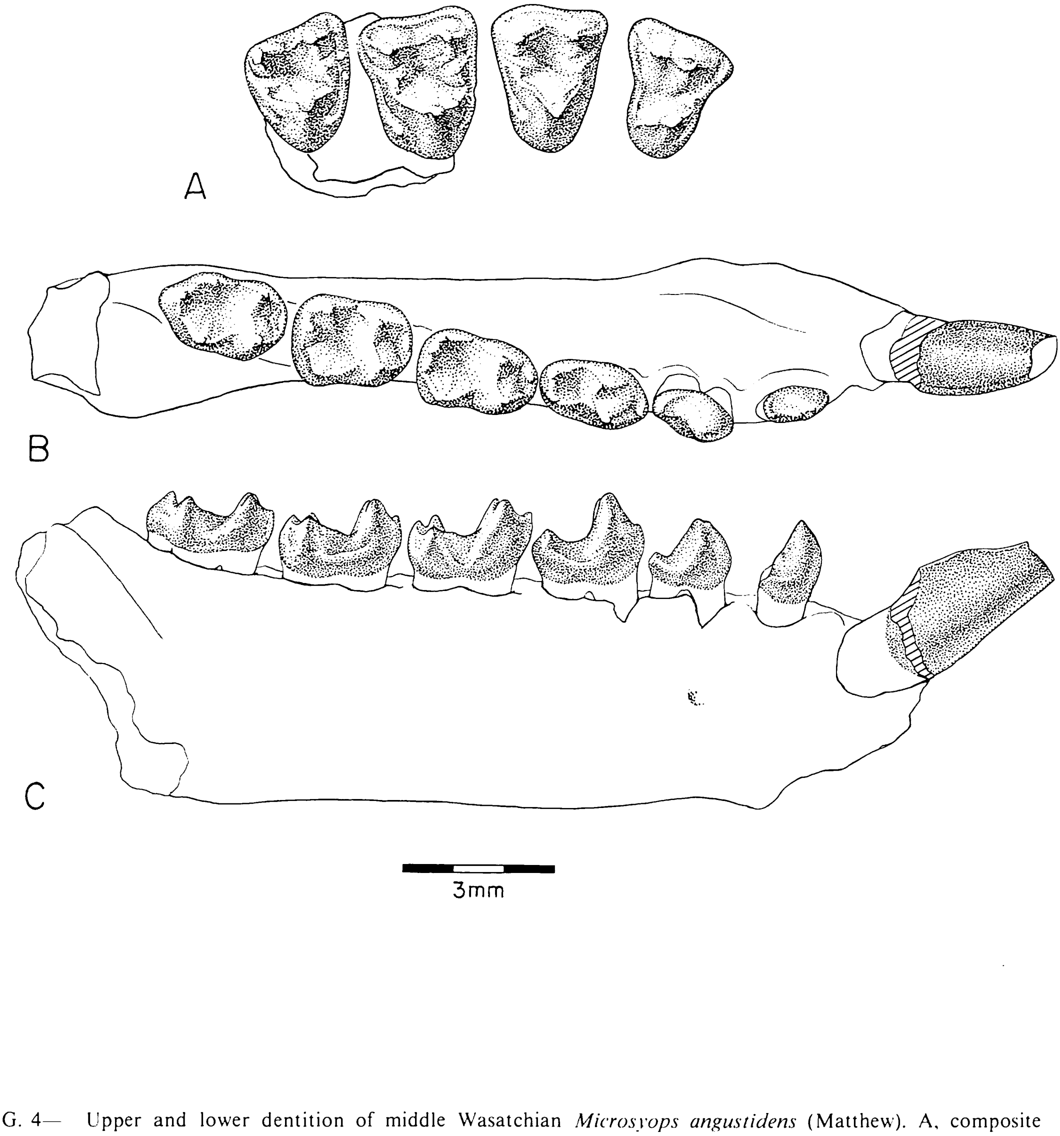


FIG. 4— Upper and lower dentition of middle Wasatchian *Microsyops angustidens* (Matthew). A, composite dentition (based on UM 73449 from UM locality SC-265, left upper P^4 and M^1, and UM 76428 from UM locality SC-253, right maxilla with M^{2-3}) in occlusal view. B, right mandible, I_1-M_3 (UM 73544), from UM locality SC-256, in occlusal view. C, same in lateral view.

shown in the same figure by McKenna (1960, p. 80, fig. 40b). Interproximal wear facets indicate that the two teeth are not from the same individual. Another P^4 from the same locality as the type (Despair Quarry) is virtually indistinguishable from that of *M. angustidens*. The P^4 figured by McKenna does not represent *Microsyops*. Thus there is no longer any basis for separating *C. alfi* from *M. angustidens*.

Hypodigm.—UM localities and specimen numbers from the Clark's Fork Basin: SC-113—66691 (RI^1, P_4), 82042 (LM^x); SC-131—79961 (L Mand P_4-M_1); SC-148—67337 (L Max M^1); SC-253—73036 (L Mand M_{1-3}), 73045 (R Max M^{1-3}), 76428 (R Max M^{2-3}), 76440 (R Mand M_2); SC-255—73093 (RP_4), 73099 (R Mand M_{1-2}), 73123 (R Mand M_{1-2}), 73140 (L Mand P_4, M_2), 73177 (R Mand M_{1-2}), 73197 (L Mand M_{1-2}), 73240 (L Mand P_4, M_2), 73250 (R Mand M_{1-2}), 73284 (R Mand M_{1-2}), 73317 (RP_4), 80102 (L Mand P_4), 80131 (RM^1), 80137 (RM_2), 80153 (LM_1), 80159 (LM_2), 82043 (RM^x); SC-256—73544 (R Mand I_1-M_3), 73545 (RM_1, LM_2), 73562 (R Mand M_{1-2}), 80856 (RM_1), 80857 (RM_1), 80858 (L Mand M_1); SC-265—73432 (L Mand P_4-M_2), 73444 (R Mand M_{1-2}), 73449 (LP^4, M^1), 73641 (L Mand P_{3-4}), 73642 (LI_1), 75648 (LI^1), 80859 (RI_1, P_4, M_1, LP_4), 80860 (R Mand M_2), 80861 (RM_1), 80862 (LM_1), 80863 (LM_1), 80864 (LM_2); SC-295—82039 (LI^1); SC-303—80741 (R Mand M_{1-2}), 80747 (R Mand M_{1-2}), 80751 (L Mand M_1), 82044 (LP_4).

Additional middle Wasatchian *M. angustidens* specimens from the Bighorn Basin include: USGS numbers 3712 (R Max P^4-M^3), 3714 (L Mand P_4-M_1), 3792 R Mand M_{1-2}), 3818 (R Mand M_{1-2}), 3826 (L Mand P_4-M_3), 6027 (R Mand M_{1-2}), 6602 (L Mand P_4-M_2), 6605 (R Mand M_{1-3}), 6606 (R Mand M_{1-3}), 6608 (L Mand P_4-M_2), 6609 (R Mand M_{1-2}), 7754 (L Mand P_3-M_2), 8014 (L Mand P_4-M_1), and others; YPM numbers 23186 (R Mand P_4-M_1), 24986 (L Mand M_1), 25001 (L Mand M_{1-3}), 25047 (R Mand M_1), 25375 (L Mand P_4), 30511 (R Mand P_4-M_2), 30517 (RM^1), 30813 (L Mand M_{1-3}), 30817 (L Mand P_4-M_2), 30830 (L Mand P_4, M_2), 32002 (L Mand M_{2-3}), and others.

Microsyops sp. A
Fig. 5

Discussion.—Three University of Michigan specimens from the Clark's Fork Basin are sufficiently distinct to warrant specific recognition. These specimens include: UM 74015, 75637, and 82596. Specific diagnosis and a description of these specimens is being prepared (Bakker and Gunnell, in preparation). USGS specimens 1375, 6320, 6322, 6323, 6598, and 6608, from the central Bighorn Basin can also be assigned to this species.

STRATIGRAPHIC DISTRIBUTION

Most studies of microsyopine evolution have emphasized the continuity of dental features that characterize this radiation (Szalay, 1969). Metaconids on lower fourth premolars, and stylar shelves and mesostyles on upper molars were thought to be added gradually during the radiation of microsyopines through the Eocene. Stratigraphic study of Clark's Fork Basin microsyopines permits a modification of this progression (see Fig. 6). Evidence now available suggests fairly rapid development of a metaconid on P_4 and, to a lesser extent, mesostyles on upper molars. At UM locality SC-111, specimens of *Arctodontomys* have no trace of a metaconid on P_4, while at UM locality SC-113, just 45 meters higher stratigraphically, specimens of *Microsyops* have a

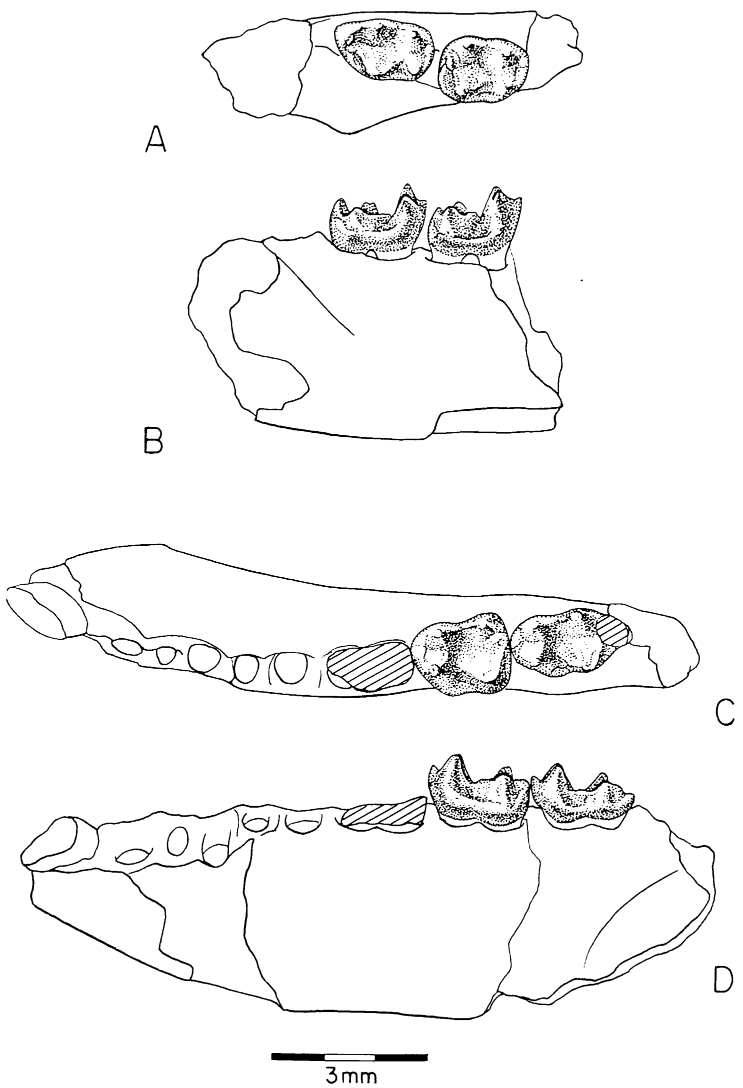
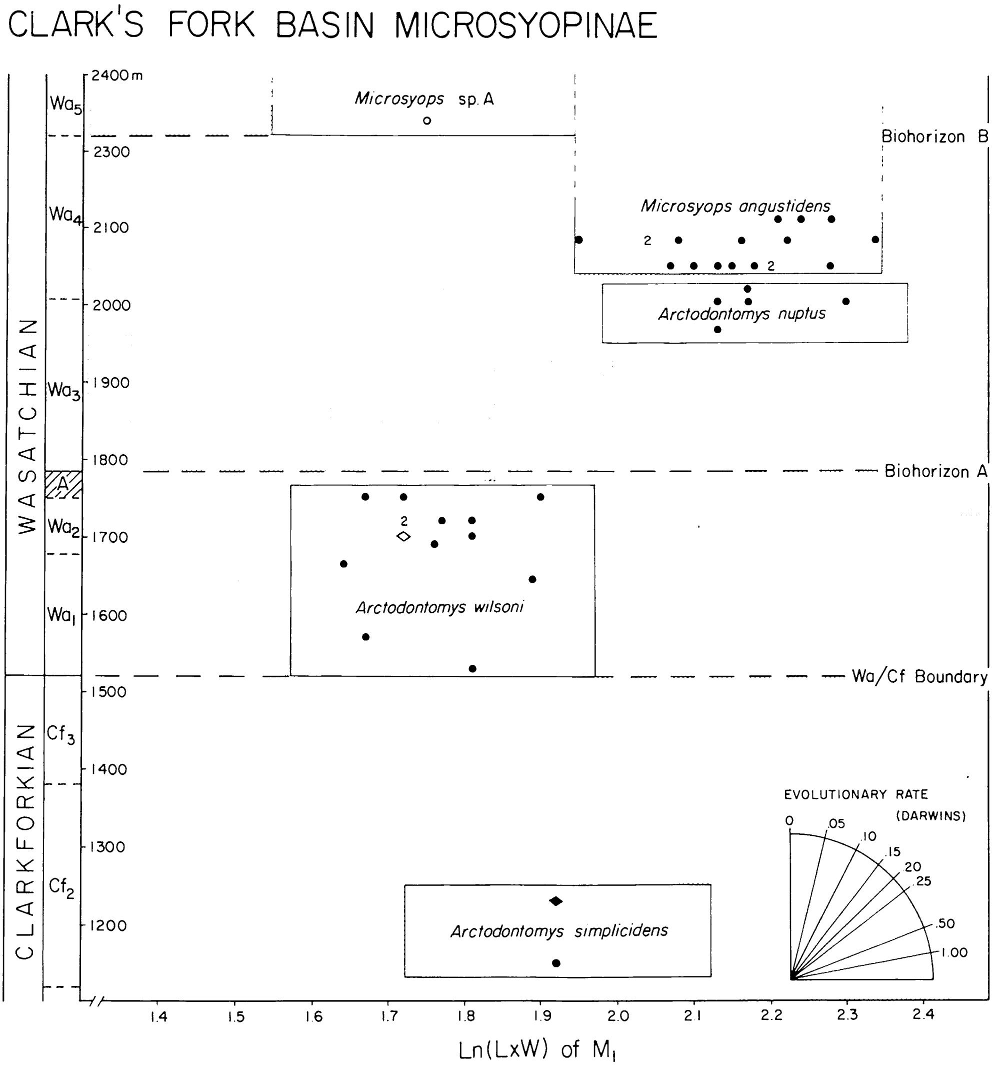


FIG. 5— Lower dentition of late middle Wasatchian *Microsyops* sp. A. A, right mandible, M_{2-3} (UM 74015), from UM locality SC-295, in occlusal view. B, same in lateral view. C, left mandible, M_{2-3} (UM 75637), from UM locality SC-302, in occlusal view. D, same in lateral view.

FIG. 6— Relative body sizes (based on tooth size) and stratigraphic ranges of early Eocene Microsyopinae in the Clark's Fork Basin. Abscissa is the natural logarithm of M_1 crown area. Ordinate is stratigraphic level in meters, measured from the base of the Paleocene Fort Union Formation on Polecat Bench. CF_2 and CF_3 are middle and late Clarkforkian, respectively. Wa_1 and Wa_2 (Sandcouleean) represent early Wasatchian, while Wa_{3-5} (early through late Graybullian) represent middle Wasatchian. Solid circles represent individual specimens of known stratigraphic level. Open circle is an approximation of M_1 size of *Microsyops* sp. A of known stratigraphic level. Numbers indicate more than one specimen of the same size from a given stratigraphic level. Solid triangle represents the holotype of *Arctodontomys simplicidens*. Open triangle represents the holotype specimen of *Arctodontomys wilsoni* from the early Wasatchian of the central Bighorn Basin. Boxes enclose recognized species, but sampling is insufficient to suggest ancestral-descendent relationships between species. The boxes enclosing *Microsyops* sp. A and *Microsyops angustidens* remain open at the top because their last appearance is not documented in the Clark's Fork Basin. The coexistence of *Microsyops* sp. A and *M. angustidens* in the same stratigraphic horizon is documented in the central Bighorn Basin. Note abrupt appearances of *Microsyops angustidens* and *Microsyops* sp. A.


CLARK'S FORK BASIN MICROSYOPINAE
WASATCHIAN
CLARKFORKIAN
Wa5
Wa4
Wa3
A
Wa2
Wa1
Cf3
Cf2
2400 m
2300
2100
2000
1900
1800
1700
1600
1500
1400
1300
1200
Microsyops sp. A
Biohorizon B
Microsyops angustidens
Arctodontomys nuptus
Biohorizon A
Arctodontomys wilsoni
Wa/Cf Boundary
EVOLUTIONARY RATE
(DARWINS)
0
.05
.10
.15
.20
.25
.50
1.00
Arctodontomys simplicidens
1.4
1.5
1.6
1.7
1.8
1.9
2.0
2.1
2.2
2.3
2.4
Ln(LxW) of M1

metaconid completely developed and distinct from the protoconid. *Arctodontomys* shows some variation in P_4 morphology. Most specimens have no trace of a metaconid, while some have a small fold of enamel developed in the position of the metaconid. In no case is there ever development of a distinct cusp. *Microsyops* also shows variation. Some specimens have small metaconids on P_4, while in others there is a metaconid of fairly large size, but in all cases a distinct cusp is present. Implications are that either (1) relatively rapid phyletic evolution has occurred over this 45 meter interval, or (2) a migration event is being sampled at this time, with forms possessing metaconids replacing those that did not possess them. One item of evidence supporting the latter suggestion is the fact that before development of metaconids on P_4, microsyopines are relatively rare, while after the appearance of this character, they become much more common. In the 270 meters of section preceding the morphological change, only 13 specimens are known from the Clark's Fork Basin, while in the 70 meters following this change 35 specimens are known. Collecting bias is an unlikely explanation, as this entire section has been rather heavily collected and if anything, the 270 meters before the morphological change has been more heavily worked than the 70 meters following the change.

The increase in numbers of microsyopine specimens (coupled with the morphological change) suggests an adaptive shift and could support the suggestion of a migrational event. On the other hand, other morphological factors are consistent with phylogenetic change. For instance, there is little or no change in M_1 size, indicating that body size over this 45 meter interval was constant, which suggests that major ecological differences do not exist between the two species. Until samples improve in this 45 meter interval, the possible explanations and mechanisms of this morphological change will have to be speculative.

Generic separation between *Arctodontomys* and *Microsyops* is warranted, not only on the evidence of the metaconid and mesostyle, but also on other less compelling but nonetheless important evidence. *Arctodontomys* specimens tend to have more acute cusp development than do specimens of *Microsyops*. Upper P^4 lacks a distinct metacone in *Arctodontomys*, although it is incipient in some cases. *Arctodontomys* tends to have a single-rooted P_3. In 75% of the known cases, P_3 has a single root, while in the other 25%, P_3 has a single root that branches into a double root at the mandibular margin (except in one case where the P_3 is clearly double-rooted). In *Microsyops*, P_3 is invariably double-rooted. *Arctodontomys* has a P_4 talonid that normally has a single cusp, centrally located, which is connected to the trigonid by a lingual cristid. In some cases a lingual cusp (entoconid) is developed on this lingual cristid. In *Microsyops* the P_4 talonid is more molariform, with a well-developed entoconid and a better formed talonid basin.

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LITERATURE CITED

BOWN, T.M. 1979. Geology and mammalian paleontology of the Sand Creek Facies, Lower Willwood Formation (Lower Eocene), Washakie County, Wyoming. Geological Survey of Wyoming, Memoir 2:1-151.

______. 1982. Geology, paleontology, and correlation of Eocene volcaniclastic rocks, southeast Absaroka Range, Hot Springs County, Wyoming. United States Geological Survey Professional Paper, 1201-A:A1-A75.

______and P.D. GINGERICH. 1973. The Paleocene primate *Plesiolestes* and the origin of Microsyopidae. Folia Primatologica, 19:1-8.

______and K.D. ROSE. 1976. New early Tertiary primates and a reappraisal of some Plesiadapiformes. Folia Primatologica, 26:109-138.

COPE, E. D. 1881. On the vertebrata of the Wind River Eocene beds of Wyoming. Bulletin of the United States Geological and Geographical Survey of the Territories, 6:183-202.

______. 1882. The fauna of the Wasatch beds of the Basin of the Big Horn River. Proceedings of the American Philosophical Society, 20:139-197.

______. 1884. The Vertebrata of the Tertiary formations of the West. Report of the United States Geological Survey of the Territories, 3:1-1009.

GAZIN, C.L. 1952. The Lower Eocene Knight Formation of western Wyoming and its mammalian faunas. Smithsonian Miscellaneous Collections, 117:1-82.

______. 1968. A new primate from the Torrejonian Middle Paleocene of the San Juan Basin, New Mexico. Proceedings of the Biological Society of Washington. 81:629-634.

______. 1976. Mammalian faunal zones of the Bridger Middle Eocene. Smithsonian Contributions to Paleobiology, 26:1-25.

GIDLEY, J.W. 1923. Paleocene primates of the Fort Union Formation, with discussion of relationships of Eocene primates. Proceedings of the United States National Museum, 63:1-38.

GINGERICH, P. D. 1976. Cranial anatomy and evolution of Early Tertiary Plesiadapidae (Mammalia, Primates). University of Michigan Papers on Paleontology, 15:1-141.

______. 1980. History of early Cenozoic vertebrate paleontology in the Bighorn Basin. *In* P.D. Gingerich (ed.), Early Cenozoic Paleontology and Stratigraphy of the Bighorn Basin, Wyoming. University of Michigan Papers on Paleontology, 24:7-24.

______. 1982. Time resolution in mammalian evolution: Sampling, lineages, and faunal turnover. Third North American Paleontological Convention, Proceedings, 1:205-210.

______. 1983. Paleocene-Eocene Faunal Zones and a preliminary analysis of Laramide Structural Deformation in the Clark's Fork Basin, Wyoming. *In* W.W. Boberg (ed.), Wyoming Geological Association, 34th Annual Field Conference Guidebook, Geology of the Bighorn Basin, 1983:185-195.

______, K.D.ROSE, and D.W. KRAUSE. 1980. Early Cenozoic mammalian faunas of the Clark's Fork Basin-Polecat Bench area, Northwestern Wyoming. *In* P.D. Gingerich (ed), Early Cenozoic Paleontology and Stratigraphy of the Bighorn Basin, Wyoming. University of Michigan Papers on Paleontology, 24:51-68.

______and A.S. RYAN. 1979. Dental and cranial variation in living Indriidae. Primates, 20:141-159.

______, B.H. SMITH, and K. ROSENBERG. 1982. Allometric scaling in the dentition of primates and prediction of body weight from tooth size in fossils. American Journal of Physical Anthropology, 58:81-100.

GRANGER, W. 1914. On the names of the lower Eocene faunal horizons of Wyoming and New Mexico. Bulletin of the American Museum of Natural History, 33:201-207.

GUNNELL, G.F. and P.D. GINGERICH. 1981. A new species of *Niptomomys* (Microsyopidae) from the early Eocene of Wyoming. Folia Primatologica, 36:128-137.

JEPSEN, G.L. 1930. Stratigraphy and Paleontology of the Paleocene of Northeastern Park County, Wyoming. Proceedings of the American Philosophical Society, 69:463-528.

KAY, R.F. and M. CARTMILL. 1977. Cranial morphology and adaptation of *Palaechthon nacimienti* and other Paromomyidae (Plesiadapoidea, ?Primates), with a description of a new genus and species. Journal of Human Evolution, 6:19-53.

KELLEY, D. R. and A. E. WOOD. 1954. The Eocene mammals from the Lysite Member, Wind River Formation of Wyoming. Journal of Paleontology, 28:337-366.

LEIDY, J. 1872. On fossil vertebrates in the Early Tertiary Formation of Wyoming. Fifth Annual Report of the United States Geological and Geographical Survey of the Territories (F.V. Hayden), pages 353-372.

LOOMIS, F. B. 1906. Wasatch and Wind River Primates. American Journal of Science, 21:277-285.

LUCAS, S. G. 1982. Vertebrate paleontology, stratigraphy, and biostratigraphy of Eocene Galisto Formation, north-central New Mexico. New Mexico Bureau of Mines and Mineral Resources, Circular 186:7-34.

MARSH, O. C. 1871. Notice of some new fossil mammals from the Tertiary Formation. American Journal of Science, 2:35-44;120-127.

______. 1872. Preliminary description of new Tertiary mammals. Parts I-IV. American Journal of Science, 4:122-128;202-224.

MATTHEW, W.D. 1915. A revision of the Lower Eocene Wasatch and Wind River faunas. Part IV. Entelonychia, Primates, Insectivora (part). Bulletin American Museum of Natural History, 34:429-483.

______and W. GRANGER. 1921. New genera of Paleocene mammals. American Museum Novitates, 13:1-7.

MCKENNA, M.C. 1960. Fossil Mammalia from the early Wasatchian Four Mile Fauna, Eocene of Northwest Colorado. University of California Publications in Geological Sciences, 37:1-130.

OSBORN, H.F. and J.L. WORTMAN. 1892. Fossil mammals of the Wasatch and Wind River beds. Collection of 1891. Bulletin of the American Museum of Natural History, 4:81-147.

ROBINSON, P. 1966. Fossil Mammalia of the Huerfano Formation, Eocene of Colorado. Peabody Museum of Natural History Bulletin, 21:1-95.

ROSE, K.D. 1981. The Clarkforkian Land-Mammal Age and mammalian faunal composition across the Paleocene-Eocene boundary. University of Michigan Papers on Paleontology, 26:1-197.

______and T.M. BOWN. 1982. New Plesiadapiform Primates from the Eocene of Wyoming and Montana. Journal of Vertebrate Paleontology, 2:63-69.

SCHANKLER, D.M. 1980. Faunal zonation of the Willwood Formation in the central Bighorn Basin, Wyoming. *In* P.D. Gingerich (ed.), Early Cenozoic paleontology and stratigraphy of the Bighorn Basin, Wyoming. University of Michigan Papers on Paleontology, 24:99-114.

SIMONS, E.L. 1972. Primate evolution: An introduction to man's place in nature. New York, Macmillan, 322 pages.

SIMPSON, G.G. 1935. New Paleocene mammals from the Fort Union of Montana. Proceedings of the United States National Museum, 83:221-244.

______. 1955. The Phenacolemuridae, new family of early Primates. Bulletin of the American Museum of Natural History, 105:411-442.

STOCK, C. 1934. Microsyopinae and Hyopsodontidae in the Sespe Upper Eocene, California. Proceedings of the National Academy of Science, 20:349-354.

______. 1938. A tarsiid primate and a mixodectid from the Poway Eocene, California. Proceedings of the National Academy of Science, 24:288-293.

SZALAY, F.S. 1969. Mixodectidae, Microsyopidae, and the insectivore-primate transition. Bulletin of the American Museum of Natural History, 140:195-330.

WHITE, T. E. 1952. Preliminary analysis of the vertebrate fossil fauna of the Boysen reservoir area. Proceedings of the United States National Museum, 102:185-207.

TABLE 1 — Species of Clarkforkian through middle Wasatchian *Arctodontomys* and *Microsyops* recognized in the Clark's Fork Basin. Valid species are numbered in the order in which they were described.

	Species	Type Locality
1.	"*Pantolestes*" *nuptus* Cope, 1882 [Now placed in *Arctodontomys*]	"Coryphodon beds," central Bighorn Basin, Wyoming
2.	*Cynodontomys angustidens* Matthew, 1915 [Now placed in *Microsyops*]	Middle Graybullian beds, central Bighorn Basin, Wyoming
	Cynodontomys alfi Mckenna, 1960 [Synonym of *Microsyops angustidens*]	Graybullian equivalent beds, Despair Quarry, Sand Wash Basin, Colorado
3.	*Microsyops wilsoni* Szalay, 1969 [Now placed in *Arctodontomys*]	Lower Graybullian beds, Willwood Formation, KU Locality 32, SW1/4, Sec. 28, T50N, R93W, South Fork Elk Creek, central Bighorn Basin, Wyoming
4.	*Microsyops simplicidens* Rose, 1981 [Now placed in *Arctodontomys*]	Lower-middle Clarkforkian beds, Willwood Formation, UM Locality SC-137, NE1/4, Sec. 1, T57N, R102W, Clark's Fork Basin, Wyoming
5.	*Microsyops* sp. A	

TABLE 2 — Summary of measurements of upper and lower teeth of *Arctodontomys simplicidens* from the Clark's Fork Basin, Wyoming. L = length, W = width, N = sample size, OR = observed range, $\overline{X}$ = mean, S = standard deviation, V = coefficient of variation. All measurements in mm.

Tooth Position		N	OR	$\overline{X}$	S	V
Upper Dentition						
M^1	L	1	2.9	-	-	-
	W	1	3.6	-	-	-
Lower Dentition						
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	0.14	4.5
	W	2	2.0-2.1	2.05	0.07	3.4
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	-	-	-

TABLE 3 — Summary of measurements of upper and lower teeth of *Arctodontomys wilsoni* from the Clark's Fork Basin, Wyoming. Abbreviations as in Table 2. All measurements in mm.

Tooth Position		N	OR	$\bar{X}$	S	V
Upper Dentition						
P^3	L	2	1.6-1.8	1.70	0.14	8.3
	W	2	1.5-1.7	1.60	0.14	8.8
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	-	-	-
Lower Dentition						
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

TABLE 4 — Summary of measurements of upper and lower teeth of *Arctodontomys nuptus* from the Clark's Fork Basin, Wyoming. Abbreviations as in Table 2. All measurements in mm.

Tooth Position		N	OR	$\overline{X}$	S	V
Upper Dentition						
M^2	L	1	3.6	-	-	-
	W	1	4.8	-	-	-
Lower Dentition						
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	0.14	3.6
	W	2	2.6	-	-	-

TABLE 5 — Summary of measurements of upper and lower teeth of *Microsyops angustidens* from the Clark's Fork Basin, Wyoming. Abbreviations as in Table 2. All measurements in mm.

Tooth Position		N	OR	$\overline{X}$	S	V
Upper Dentition						
P^4	L	1	3.10	-	-	-
	W	1	3.30	-	-	-
M^1	L	1	3.40	-	-	-
	W	1	3.70	-	-	-
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	3.2-3.3	3.25	0.07	2.2
	W	2	3.7-4.0	3.85	0.21	5.5
Lower Dentition						
P_2	L	1	1.90	-	-	-
	W	1	1.20	-	-	-
P_3	L	2	2.3-2.5	2.40	0.14	5.9
	W	2	1.4	-	-	-
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	-	-	-