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Philip D. Gingerich, Director

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SYSTEMATICS AND EVOLUTION OF EARLY EOCENE HYAENODONTIDAE (MAMMALIA, CREODONTA) IN THE CLARKS FORK BASIN, WYOMING

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Abstract.— Study of a large new collection of early Eocene carnivorous mammals from the Clarks Fork Basin, Wyoming, required extensive review of all early Eocene Hyaenodontidae. The type specimen (now lost) of the first early Eocene hyaenodontid described from North America, *Prototomus viverrinus*, was ambiguously described by E. D. Cope. This species is regarded as a small middle-to-late Wasatchian hyaenodontine rather than a limnocyonine or miacid to conserve the generic name *Prototomus* and retain its conventional constitution. Seven genera and seventeen species are recognized here, representing a minimum of eleven distinct lineages of Hyaenodontidae in the early Eocene of North America: *Prototomus* with seven species (three new), *Tritemnodon?* with one species, *Prolimnocyon* with three species (one new), *Arfia* with three species (one new), *Galecyon* (new genus) with one species, *Acarictis* (new genus) with one species (new), and *Pyrocyon* (new genus) with one species (new). *Arfia shoshoniensis* and *Prototomus martis* are represented by several fragmentary but informative partial skeletons indicating that they were cursorial predators capable of extreme plantar flexion and inversion of the hind feet. Hind foot reversal is an ability associated with arboreality. Evolutionary patterns observed in early Eocene Hyaeodontidae can all be explained by gradual evolution at relatively low rates. Abrupt appearance of six hyaenodontid lineages in the Clarks Fork Basin at or near the beginning of the Wasatchian land-mammal age indicates that the family originated and diversified somewhere else, possibly in Africa.

INTRODUCTION

Creodonts are extinct carnivorous mammals that diversified during the early Cenozoic. They were important mammalian predators during the Eocene on all northern continents. Two families are commonly included in the order: Oxyaenidae, with two well developed shearing carnassial teeth (M^{1-2} or M_{1-2}) in each jaw quadrant, and Hyaenodontidae, with three carnassials (M^{1-3} or M_{1-3}) in each jaw. The oldest hyaenodontids from North America are found in early Wasatchian sediments, which are best known in the Sand Coulee area of the Clarks Fork Basin in northwestern Wyoming. A minimum of eight evolutionary lineages are represented, and three of these represent new genera.

This is the first substantial revision of early Eocene Hyaenodontidae since Matthew (1915). With the benefit of some 360 new specimens, it is possible to identify several new lineages and to clarify the distinctiveness of several of Matthew's lineages. We are reasonably confident of the history of early Wasatchian hyaenodontids in the Clarks Fork Basin because these are so well sampled, but we are less sure of our interpretations of middle and late Wasatchian hyaenodontids from the central Bighorn Basin and elsewhere. New middle and late Wasatchian collections have been made in recent years, and hopefully these will be studied soon to clarify remaining problems.

This is the third in a series of reviews of late Paleocene and early Eocene carnivorous mammals (Gingerich, 1983; Gingerich and Winkler, 1985). We include the previously unpublished hyaenodontid systematics of Deutsch (1979), extensively modified to accommodate many new specimens collected subsequently. Evolutionary conclusions are based primarily on Clarks Fork Basin specimens because the Clarks Fork Basin has the densest hyaenodontid stratigraphic record for the early and middle parts of the early Eocene. University of Michigan specimens from the San Juan Basin, New Mexico, and the central Bighorn Basin, Wyoming, are also described here, and specimens from other areas are discussed when appropriate. University of Michigan specimens from the Foster Gulch and McCullough Peaks areas of the northern Bighorn Basin are included in tables of measurements.

MEASUREMENTS AND ABBREVIATIONS

Dental measurements are outlined in Figure 1. All measurements were made by the senior author using dial calipers. Tables of measurements are collected at the end of the text.

Museum abbreviations are as follows:

ACM — Amherst College Museum, Amherst, Massachusetts.
AMNH — American Museum of Natural History, New York.
MNHN — Muséum National d'Histoire Naturelle, Paris.
UA — University of Alberta, Edmonton.
UM — University of Michigan Museum of Paleontology, Ann Arbor.
USNM — United States National Museum, Smithsonian Institution, Washington.
UW — University of Wyoming Geological Museum, Laramie.
YPM — Yale University Peabody Museum, New Haven.
YPM-PU — Princeton University collection at the Yale Peabody Museum, New Haven.

HISTORY OF STUDY

North American early Eocene Hyaenodontidae have a complex history of discovery and description. The family was first proposed by Leidy (1869, p. 38) to distinguish archaic carnivorous *Hyaenodon* from other contemporary mammals. Leidy later described the new genus and species *Sinopa rapax* from the Bridgerian middle Eocene of North America, but he did not recognize this as a hyaenodontid (Leidy, 1871). Cope named the new genus and species *Stypolophus pungens* from the Bridgerian middle Eocene (Cope, 1872) and the new genus and species *Prototomus viverrinus* from the Wasatchian early Eocene (Cope, 1874). The following year Cope (1875) described three additional species of *Prototomus*: *P. secundarius*, *P. multicuspis*, and *P. strenuus*. By the time he illustrated specimens of *Prototomus*, this genus was synonymized with *Stypolophus* (Cope, 1877). Later Scott (1892) synonymized both *Stypolophus* and *Prototomus* with *Sinopa.*

Cope (1875b) proposed Creodonta as a new suborder of carnivorous Insectivora distinct from true Carnivora to include North American *Ambloctonus*, *Oxyaena*, *Stypolophus*, and *Didymictis*, and European *Palaeonictis* and *Pterodon*. Thus, from the beginning, Creodonta was based principally on genera now included in either Oxyaenidae or Hyaenodontidae, the one exception being *Didymictis*. Schlosser (1886, p. 292-293) regarded Leidy's Hyaenodontidae as specialized advanced creodonts derived from mesonychids, and proposed a new family Proviverridae to include primitive genera: *Proviverra* from Europe, and *Styplolophus* (=*Prototomus*) from North America (other genera were included as well).

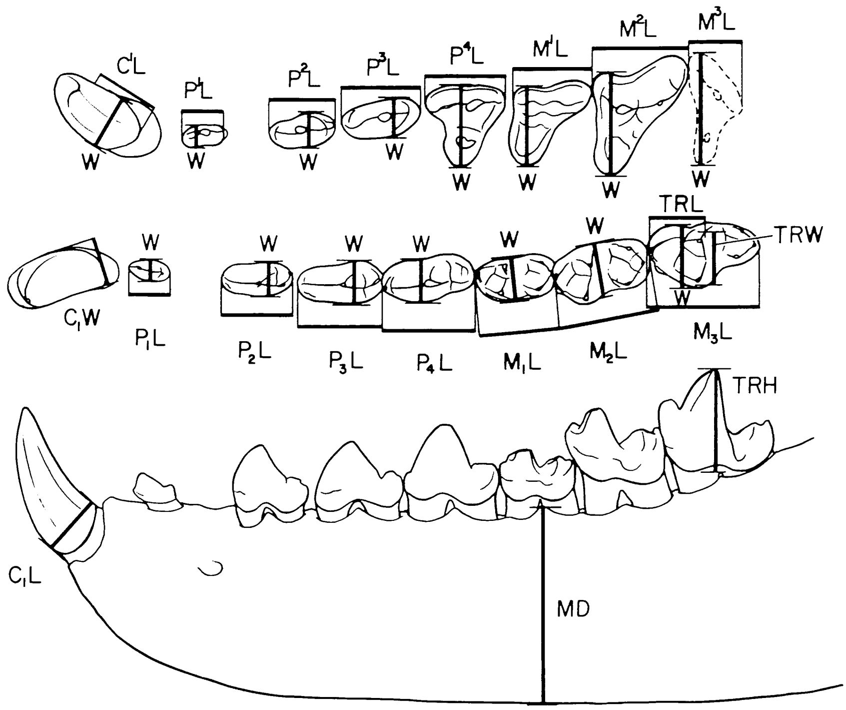

FIG. 1— Outline drawings of upper and lower cheek teeth of *Arfia* sp. to illustrate measurements employed here. Note multiple measurements of M_3, which is often the most distinctive tooth characterizing different hyaenodontid species and also usually the least worn. *L* = crown length, *MD* = mandibular depth measured labially beneath M_1, *TRH* = trigonid height, *TRL* = trigonid length, *TRW* = trigonid width, and *W* = crown width.

Matthew (1915) recognized two genera and ten species of Hyaenodontidae in the North American early Eocene: *Sinopa* with nine species, and *Tritemnodon* with one species. Matthew (1915) proposed a new genus, *Prolimnocyon*, for three early Eocene species considered to be oxyaenids. *Sinopa* Leidy, 1871, is based on the Bridgerian middle Eocene species *Sinopa rapax* Leidy (1871), while *Tritemnodon* Matthew, 1906, is based on Bridgerian *Limnocyon agilis* Marsh (1872). Gazin (1952) proposed a fourth and Guthrie (1967b) a fifth species of North American early Eocene *Prolimnocyon*. In the mean time, Van Valen (1965) restricted *Sinopa* to include only middle Eocene species and simultaneously synonymized it with European *Proviverra* (a questionable synonymy not widely followed). He placed two of the North American early Eocene species recognized by Matthew in a new genus *Arfia*, five North American early Eocene species in Cope's genus *Prototomus*, and three North American early Eocene species in Matthew's genus *Tritemnodon*. All of these species are listed in Table 1.

TABLE 1 — Summary of the early Eocene hyaenodontid species described from North America. Species are listed in the order in which they were described. Those considered valid are numbered at the left. Basin abbreviations are as follows: BHB, Bighorn Basin; CFB, Clarks Fork Basin; GRB, Green River Basin; SJB, San Juan Basin; and WRB, Wind River Basin.

Species	Type specimen	Type locality	Additional references
1. *Prototomus viverrinus* Cope, 1874, p. 13 [Type species of *Prototomus*]	USNM 1022 (lost) $M^2 = 5.0 \times 6.8$	Arroyo Blanco, SJB Grayb.-Lysitean	Matthew, 1915, p. 83 Simpson, 1951, p. 15
Prototomus insidiosus Cope, 1874, p. 14 [Type sp. of condylarth *Apheliscus* Cope, 1875]	USNM (lost)	Arroyo Blanco, SJB Grayb.-Lysitean	Matthew, 1918, p. 596 Simpson, 1951, p. 15
Prototomus jarrovii Cope, 1874, p. 14 [Type sp. of primate *Pelycodus* Cope, 1875]	USNM (lost)	Arroyo Blanco, SJB Grayb.-Lysitean	Matthew, 1915b, p. 438 Simpson, 1951, p. 15
2. *Prototomus secundarius* Cope, 1875, p. 9	USNM 1025 $M_2 = 7.5 \times 3.3$	Arroyo Almagre?, SJB Grayb.-Lysitean	Matthew, 1915, p. 82 Simpson, 1951, p. 16
Prototomus multicuspis Cope, 1875, p. 10 [Synonym of *Prototomus secundarius*]	USNM 1021 $M^2 = 7.0 \times 9.0$	Arroyo Almagre?, SJB Grayb.-Lysitean	Matthew, 1915, p. 80 Simpson, 1951, p. 16
3. *Prototomus strenuus* Cope, 1875, p. 10 [Now placed in *Tritemnodon?*]	USNM 1023 $M_2 = 8.0 \times 6.5$	Arroyo Almagre?, SJB Grayb.-Lysitean	Matthew, 1915, p. 74 Simpson, 1951, p. 16
Stypolophus hians Cope, 1877, p. 118 [Synonym of *T.? strenuus*]	USNM 1111	Arroyo Almagre?, SJB Grayb.-Lysitean	Matthew, 1915, p. 75 Simpson, 1951, p. 16
Stypolophus whitiae Cope, 1882, p. 161 [Probable synonym of *T.? strenuus*]	AMNH 4781	"Wind River Basin" Lostcabinian	Matthew, 1915, p. 84
4. *Sinopa opisthotoma* Matthew, 1901, p. 28 [Type species of *Arfia* Van Valen 1965]	AMNH 99 $M^2 = 12.0 \times 13.0$	"Bighorn Basin" M. Graybullian	Matthew, 1915, p. 73
5. *Prolimnocyon atavus* Matthew, 1915, p. 68 [Type sp. of *Prolimnocyon* Matt. 1915]	AMNH 16816 $M_2 = 6.2 \times 4.0$	Head 10 Mile Cr., BHB, M. Grayb.	Gazin, 1962, p. 54. Delson, 1971, p. 334
6. *Prolimnocyon robustus* Matt., 1915, p. 70 [Here placed in *Prototomus*]	AMNH 15168	L. Fks. Dorsey Cr., BHB, M. Grayb.	AMNH catalogue
7. *Prolimnocyon antiquus* Matt., 1915, p. 70	AMNH 14768	Wind River Basin Lostcabinian	Gazin, 1962, p. 54
8. *Sinopa mordax* Matthew, 1915, p. 73 [Type species of *Galecyon*, new genus]	AMNH 16157 $M_2 = 7.8 \times 4.5$	5 mi. SE m. P. O'Hara Ck., CFB, Sandcoul.	Delson, 1971, p. 332
9. *Sinopa shoshoniensis* Matt., 1915, p. 73 [Now placed in *Arfia*]	AMNH 16158 $M_2 = 9.1 \times 4.4$	5 mi. SE m. P. O'Hara Ck., CFB, Sandcoul.	Delson, 1971, p. 330
10. *Sinopa vulpecula* Matthew, 1915, p. 80 [Questionably referred to *Prototomus*]	AMNH 15606	5 mi. N Parker Spg., BHB, Lostcabinian	
Prolimnocyon elisabethae Gazin, 1952, p. 51 [Probable synonym of *Prol. antiquus*]	USNM 19350 $M_2 = 6.8 \times 3.5$	5 mi. SE Big Piney, GRB, Lostcabinian	Gazin, 1962, p. 54
Paeneprol. amissadomus Guthrie, 1967 [Syn. of miacid *Oodectes herpestoides*]	AMNH 55559	Buck Spring, WRB Lostcabinian	MacIntyre and Guthrie, 1979, p. 1034
Prolimnocyon iudei Guthrie, 1967b, p. 14 [Synonym of miacid *Oodectes jepseni*]	ACM 2767 $M_2 = 4.4 \times 2.9$	Locality 6c, WRB Lysitean	
11. *Acarictis ryani* new genus and species	UM 79081 $M_2 \approx 4.3 \times 2.6$	SC-161, CFB Sandcouleean	
12. *Arfia zele* new species	UM 69372 $M_2 = 7.3 \times 4.3$	SC-40, CFB Sandcouleean	
13. *Prototomus deimos* new species	UM 79612 $M_2 = 5.1 \times 3.2$	SC-213, CFB E. Graybullian	
14. *Prototomus phobos* new species	YPM-PU 13019 $M_2 = 5.7 \times 3.9$	S. Dorsey Cr., BHB Graybullian	
15. *Prototomus martis* new species	UM 87317 $M_2 = 7.4 \times 4.7$	FG-103, BHB E. Graybullian	
16. *Pyrocyon dioctetus* new genus and species	UM 94757 $M_2 = 7.1 \times 4.4$	MP-193, BHB L. Graybullian	
17. *Prolimnocyon haematus* new species	UM 65622 $M_2 = 4.8 \times 3.0$	SC-54, CFB Sandcouleean	

SYSTEMATIC POSITION OF *PROTOTOMUS*

Prototomus is problematical because it is based on a type species, *Prototomus viverrinus*, that is based in turn on an indeterminate type specimen. The holotype is a partially prepared rostrum or palate illustrated by Cope (1877, Plate 38:1). Postcranial remains included with the type material must be considered questionably referred because Cope (1877, p. 113) stated that a lower jaw of similar size accompanied the palate but the lower jaw was subsequently removed to a different (unspecified) taxon and the postcranial remains may represent this second taxon too.

Cope (1877, p. 113) provided measurements of teeth in the holotype of *Prototomus viverrinus*, as follows:

Length of the last five molars	25.0 mm
Length of the true-molar series	13.5
Length of the last premolar	6.0
Width of the same	5.0
Length of the penultimate molar	5.0
Width of the same	6.8
Width of the last molar	4.7

Measurements can also be taken from Cope's illustration, printed natural size, and most of these agree with measurements printed in Cope's text. The width of the last premolar (P^4?) is a conspicuous exception, with the illustration showing a much narrower tooth than suggested by the measured width. Cope appears to have measured the overall length of the last five molars including spaces that now separate teeth (due to postmortem expansion of bone with mineral precipitation in cracks), while he appears to have reduced the length of the true-molar series to correct for these spaces. The measured length of the last premolar agrees with that in the illustration, while the measured width is greater than that illustrated. Damage to the stylar cusps of the penultimate molar (M^2?) may account for an anomalously small measured length published for this tooth. Finally, the illustration shows that the last molar (M^3?) is clearly broken, raising questions about how the published width was measured.

The holotype rostrum or palate of *Prototomus viverrinus*, part of USNM 1022, is now lost (Gazin, 1962). Matthew (1915) evidently had access to the holotype and he indicated that characters of the premolars were "suggestive of the smaller Limnocyoninae," noting that two or three fragments of lower jaws formerly thought to belong to *P. viverrinus* were now identified as *Prolimnocyon* (Matthew, 1915, p. 83— sixteen pages after describing *Prolimnocyon* as a new genus). McKenna (1960) removed *Prototomus* from synonymy with *Sinopa* and regarded it as a senior synonym of Matthew's *Prolimnocyon*, citing Cope's indication of a contracted muzzle, a wide frontal region, and a reduced M^3. Van Valen (1967) further noted, judging from Cope's illustration, that the holotype could possibly represent a miacid carnivore.

Van Valen (1967) asked the International Commission on Zoological Nomenclature [ICZN] to designate the dentary USNM 22456 as a neotype to replace the lost palate. This dentary was described and questionably referred to *Prototomus viverrinus* by Gazin (1962), but it later proved to represent a new species of the didymoconid genus *Wyolestes* (Gingerich, 1982). Van Valen's request for designation of a neotype was declined in ICZN Opinion 1263 (dated December, 1983).

Careful examination of Cope's figure of the holotype of *Prototomus viverrinus*, and comparison with known upper dentitions of contemporaneous carnivorous mammals of similar size, convinces me that *Prototomus viverrinus* is a hyaenodontid rather than a miacid or a didymoconid. However, the holotype appears to have features of several different early Eocene hyaenodontids. The reduced M^3 is, as McKenna noted, very reminiscent of that in *Prolimnocyon*, and the measurement given for the width of P^4 is like that of middle or late early Eocene *Prolimnocyon*. Reduction of M^3 could indicate relationship to the genus here named *Galecyon*. The proportions

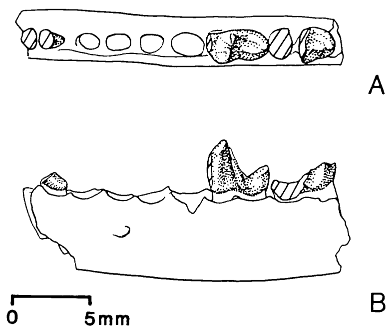

FIG. 2— Left dentary of *Acarictis ryani*, UM 79081 (holotype) from SC-161, with posterior part of crown of P_2, nearly complete crown of M_1, and talonid of M_2. A, occlusal, and B, lateral view.

of P^4 shown in Cope's illustration are most like those of the genus here named *Acarictis*, while the overall size of the specimen is most like that of a new small species in a group otherwise without certain generic attribution.

Published measurements and illustrations of the holotype of *Prototomus viverrinus* appear not to match those of any single genus of early Eocene hyaenodontid to the exclusion of all others. The holotype palate, if rediscovered, might be adequate to indicate which, if any, of the known genera is represented. However, similarity cannot be evaluated without having the holotype in hand to see which measurements and tooth proportions, if any, are affected by breakage. Without the holotype, the problem appears insoluble.

Prototomus viverrinus is here considered to represent the group of species most commonly found in the early and middle Wasatchian, in part because this is the group most commonly found (thus it is likely to be the group Cope first encountered), but also because this group currently lacks any other generic attribution. If rediscovery of the holotype should prove this assignment to be unwarranted, then a new genus will have to be proposed. In the meantime, *Prototomus* is conserved and it retains its conventional constitution

SYSTEMATIC PALEONTOLOGY

Order CREODONTA Cope, 1875
Family HYAENODONTIDAE Leidy, 1869
Subfamily PROVIVERRINAE Schlosser, 1886

Proviverrinae are distinguished from Hyaenodontinae in retaining distinct protocones, paracones, and metacones on upper molars, and in retaining metaconids on lower molars. Proviverrinae differ from Limnocyoninae in retaining an M_3 similar in size and proportion to preceding lower molars.

Acarictis, new genus

Type species.— *Acarictis ryani*, new species.

Included species.— Type species only.

Age and distribution.— Early Wasatchian land-mammal age, early Eocene, of western North America.

Diagnosis.— Differs from all other North American Hyaenodontidae in being smaller and in having a simple trigonid on M_1, with the principal cusps being about equidistant from each other. The paraconid and metaconid appear to have been about equal in size and both were smaller than the protoconid (the paraconid is not well preserved in any specimen). Upper P^3 differs from those in larger hyaenodontids in being relatively long and narrow, with a high pointed buccal cusp and a small but distinct lingual cusp. Other differences are summarized in the key in Figure 27.

Etymology.— *Acarē*, small, and *ictis*, weasel (Gr., fem.).

Discussion.— This genus is distinctive in being the smallest North American proviverrid.

Acarictis ryani, new species

Fig. 2

Holotype.— UM 79081, left dentary with part of the crown of P_2, intact crown of M_1, and part of the crown of M_2.

Type locality.— University of Michigan locality SC-161 in the Clarks Fork Basin: SE$\frac{1}{4}$, NW$\frac{1}{4}$, Section 3, T55N, R101W, Park County, Wyoming.

Age and distribution.— Middle and late Sandcouleean subage of Wasatchian land-mammal age, early part of the early Eocene, Clarks Fork Basin, Wyoming.

Diagnosis.— As for the genus.

Etymology.— Named for Mr. William Ryan, who collected the holotype in 1982.

Included specimens.— Sand Coulee area localities— SC-38: UM 75805. SC-46: UM 86291. SC-161: UM 79081 (holotype). SC-316: UM 80195.

Description.— The holotype is a left dentary preserving the posterior part of P_2, alveoli for P_3 and P_4, a nearly intact crown of M_1, and the anterior root and talonid of M_2. The trigonid of M_1 has the three principal cusps positioned about equidistant from each other. The paraconid is broken, but the remaining part of it indicates a cusp about the same size as the metaconid. Both internal cusps are smaller than the protoconid. The talonid is narrow, but about the same length as the trigonid. It is distinctly basined, as in other small proviverrines, with a straight hypoconid crest defining the labial side of the basin, and a curved entoconid-hypoconulid crest defining the lingual side. The talonid of M_2 is similar, but a little broader than that of M_1. The talonid of M_2 preserves a large interproximal wear facet on its posterior surface, indicating the presence of a sizable M_3 in life. The dentary of the holotype is shallow, and there is a large mental foramen on the labial side of the dentary beneath the posterior alveolus for P_3.

Referred specimens show that P_1 was single-rooted and that all the lower cheek teeth were closely spaced without significant diastemata. There is a large mental foramen below P_1 in addition to that below the posterior alveolus of P_3 in UM 86291, and this specimen has the shallow and relatively smooth mandibular symphysis well preserved. UM 86291 also includes a nearly intact crown of P^3, which shows the long narrow shape mentioned in the generic diagnosis above. P^3 retains a very small protocone cuspule on the lingual side of the tooth. Each of the referred specimens preserve the base of the trigonid of M_2, which appears to have been significantly wider than the trigonid of M_1 in each case. Each of the referred specimens preserves part of the anterior alveolus for M_3, indicating that this tooth was present in life. This alveolus is sufficiently well preserved in UM 80195 to indicate that M_3 was probably about the same size as M_2.

Measurements of the holotype and referred specimens are given in Table 2.

Discussion.— *Acarictis ryani* is distinctly smaller than any other North American early Eocene hyaenodontid. It may be confused with *Didelphodus absarokae*, a didelphodontine palaeoryctid with cheek teeth of similar size found in the same stratigraphic interval, but *Acarictis* differs from *Didelphodus* in having a much shallower dentary, and a smoother, less tightly joined mandibular symphysis. It differs dentally in having higher protoconids and narrower trigonids and talonids, but these macroscopic features of the dentary distinguish the two genera when teeth are poorly preserved.

Some of the very small unnamed European "Créodontes indéterminés" described by Teilhard de Chardin (1927, p. 20) and by Quinet (1968, pp. 37-38) may belong in *Acarictis.*

Arfia Van Valen, 1965

Type species.— *Sinopa opisthotoma* Matthew, 1901.

Included species.— *Arfia zele*, new species; *A. shoshoniensis* (Matthew, 1915); *A. opisthotoma,* (Matthew, 1901).

Age and distribution.— Early Wasatchian (Sandcouleean through middle Graybullian) of western North America; early Sparnacian of Europe.

Diagnosis.— Differs from all other early Eocene proviverrines in having the paracone and metacone well separated on upper molars. Differs from all proviverrines, including middle Eocene *Sinopa* in having a distinctive arcuate postmetacrista on M^{1-2}. Further differs from most North American proviverrines in having finely crenulated ("rugulose," following Matthew, 1915) rather than smooth enamel on all cheek teeth, and in having broad, squared, basined talonids on lower molars. Other differences are summarized in the key in Figure 27.

Discussion.— *Arfia* makes its first appearance in the earliest Wasatchian stratigraphic interval of the Clarks Fork Basin, Wyoming. It is the largest and the most commonly collected hyaenodontid found in Sandcouleean (early Wasatchian) through middle Graybullian (middle Wasatchian) strata. *Arfia* appears to have become extinct, locally at least, at the end of the *Haplomylus-Ectocion* range zone of Schankler (1980), when both *Haplomylus* and *Ectocion* disappeared as well. Thus *Arfia* is, on present evidence, a useful stratigraphic index fossil. Progressive morphological change in the species of *Arfia* further enhances its stratigraphic importance (and evolutionary interest).

Lange-Badré and Godinot (1982) described a species, *Arfia* "*woutersi*," from the early Sparnacian locality of Dormaal in Belgium. The hypodigm consisted of four isolated teeth. No holotype was designated, and the "syntypes" clearly represent two different taxa. *Arfia* is probably present at Dormaal, but it is not clear that *A. woutersi* is the appropriate name for the Dormaal species.

Arfia zele, new species

Fig. 3

Arfia shoshoniensis (in part), Delson, 1971, p. 329.
Arfia opisthotoma (in part), Bown, 1979, p. 87.

Holotype.— UM 69372, left dentary with M_{2-3} and associated right dentary with P_4-M_2, collected by B. Holly Smith.

Type locality.— University of Michigan locality SC-40 in the Clarks Fork Basin: NE$\frac{1}{4}$, NE$\frac{1}{4}$, Section 23, T56N, R102W, Park County, Wyoming.

Age and distribution.— *Arfia zele* is known only from the Sandcouleean subage of the Wasatchian land-mammal age, early Eocene, and it is known with certainty only from the Clarks Fork Basin, Wyoming.

Diagnosis.— Differs from *A. shoshoniensis* and *A. opisthotoma* in being about 13% smaller. Further differs from *A. opisthotoma* in having a relatively shorter, broader, less open trigonid on M_3.

Etymology.— Greek *zēlē*, rival or competitor,

Included specimens.— Foster Gulch area localities— FG-20: UM 76147. FG-42: UM 77213. FG-62: UM 85292. FG-65: UM 85358. Sand Coulee area localities— SC-4: 80766. SC-6: UM 66340, 68011, 68015, 79414, and 87832. SC-26: UM 65328 and 67389. SC-40: UM 65391 and

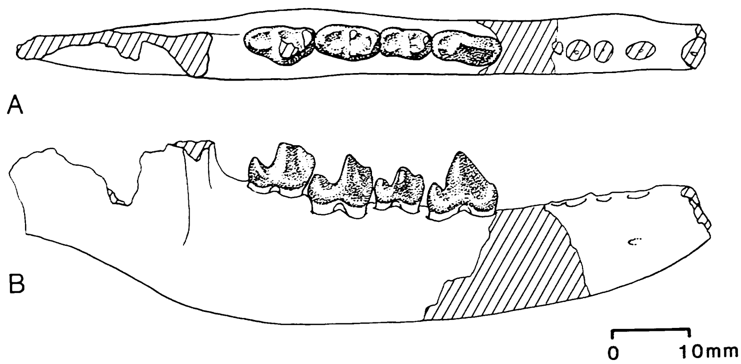

FIG. 3— Right dentary of *Arfia zele*, UM 69372 (holotype) from SC-40, with posterior alveolus of canine, alveolus for single-rooted P_1, alveoli for double-rooted P_2, missing bone, and intact crowns of P_4-M_3 (M_3 restored from associated left dentary). A, occlusal, and B, lateral view.

69372 (holotype). SC-123: UM 76684. SC-124: UM 76451 and 76453. SC-125: UM 66890. SC-142: UM 67263. SC-182: UM 68769. SC-288: UM 73783.

Description.— Maxillae of *Arfia zele* are rare, the best being UM 68769. Most specimens, like the holotype (Fig. 3), are dentaries of adult individuals. Two are dentaries of juveniles: UM 67389 has P_3 and M_3 beginning to erupt, with P_4 still in the crypt. UM 80766 has P_3 erupting slightly ahead of P_4. Some limited postcranial material is included in UM 76684 and UM 77213.

The best upper dentition is preserved in UM 68769. The left premaxilla preserves roots for all three incisors, and crowns of I^{2-3} are intact. Each has a bluntly pointed central cusp flanked by smaller medial and lateral mammalons. I^1 is the smallest incisor with the smallest root, and I^3 is the largest. The C^1 root is preserved in place in the right maxilla, followed by roots for double-rooted P^{1-2} and crowns of double-rooted P^3 and triple-rooted P^4 and M^1. C^1 is preserved in several other specimens, although not in place in the maxilla. It differs from C_1 in having a large and relatively straight root. P^3 lacks a protocone, while P^4 has a large distinct protocone. The crown of M^1 is well preserved, with a large protocone, paracone, and metacone, and the distinctive arcuate postmetacrista characteristic of the genus. M^{2-3} are missing in UM 68769, but well preserved in UM 77213. M^2 resembles M^1 but differs in being larger and in having a more exaggerated postmetacrista. M^3 is smaller, with a distinct preparacrista but a reduced metacone and no postmetacrista.

UM 68769 preserves the crowns of two lower incisors, probably left and right I_2. These resemble crowns of upper incisors, except that the medial mammalon appears reduced relative to the central cuspule and lateral mammalon. The root of I_1 is preserved on the left side. There were almost certainly three lower incisors opposing the three upper incisors. The crown of C_1 is preserved in place in UM 77213. It has a more slender curving crown set at an angle of about 60° to the root. P_1 is single-rooted and forwardly inclined, with a small simple crown. The remainder of the cheek teeth are two-rooted. P_{1-3} have simple crowns with a large central cusp, a small anterior basal cuspule or cusp, and a distinct posterior cusp. The talonid is slightly basined on P_4. Enamel on the lower premolars is distinctly crenulated. M_1 and M_2 have crowns that are nearly rectangular in occlusal outline, with a relatively low trigonid and a relatively wide talonid. M_3 is typical of carnassial teeth in other hyaenodontids in having a higher protoconid and a relatively narrower talonid than is seen on M_1 or M_2. The paraconid, protoconid, and metaconid form a more nearly equilateral triangle in *Arfia zele* than they do in later species.

Measurements of the holotype are given in Table 3, and a statistical summary of dental measurements for the species is given in Table 4. Coefficients of variation of the lengths and widths of most cheek teeth are within the 4-8 range observed in modern carnivore species (Gingerich and Winkler, 1979).

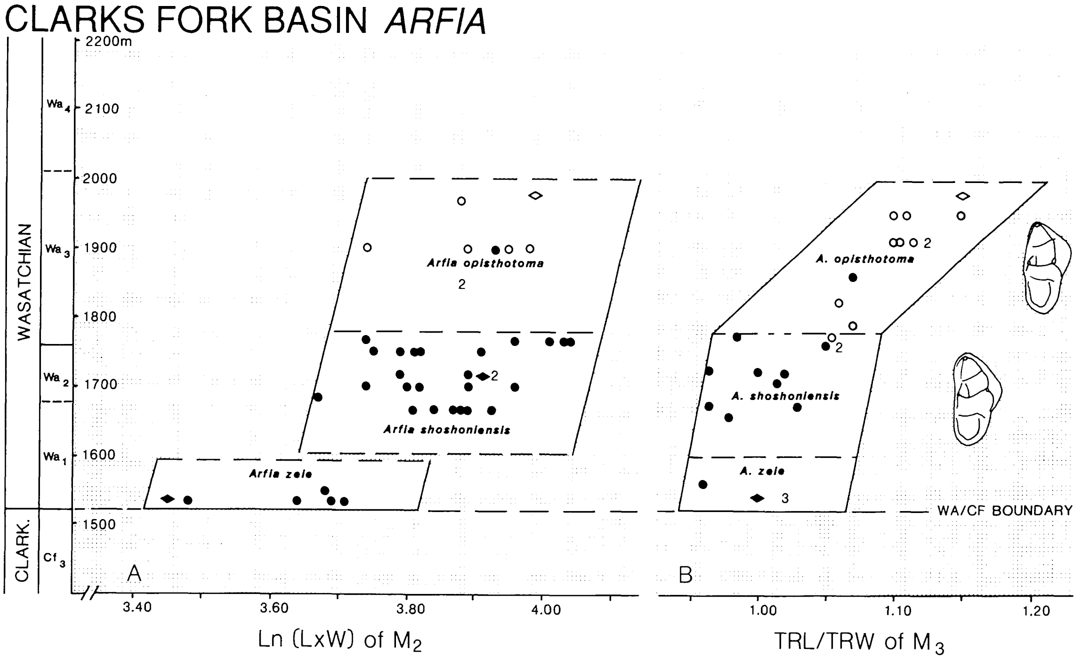

FIG. 4— Size-time and shape-time plots showing the stratigraphic distribution of early Eocene *Arfia* in the Clarks Fork Basin, Wyoming. Abscissa in figure at left (A) is size of M_2 as an indicator of overall body size. Size of M_2 is plotted rather than M_1 because M_2 is usually much less worn in hyaenodontids. Abscissa in figure at right (B) is M_3 trigonid length divided by M_3 trigonid width as an indicator of tooth shape. Ordinate is meter level in Clarks Fork Basin stratigraphic section. Solid figures and associated integers represent specimens from known stratigraphic levels in the Clarks Fork Basin (integers indicate multiple specimens falling at same point). Open figures and associated integers represent specimens for which stratigraphic level must be inferred by faunal comparison (specimens from localities SC-128 and SC-196). Diamonds show positions of type specimens. Dashed lines show approximate limits of mean ± two standard deviations in tooth size or shape, fit to observed distributions of points. *Arfia* made its first appearance at the beginning of the Wasatchian land-mammal age. Note that *Arfia zele* differs from later *A. shoshoniensis* and *A. opisthotoma* in being significantly smaller. *Arfia zele* and *A. shoshoniensis* both differ from *A. opisthotoma* in M_3 trigonid shape.

Postcranial remains are preserved in UM 77213. These include a nearly complete humerus measuring 88 mm in length, and 6.7 by 9.3 mm in midshaft diameter. Breadth of the distal end cannot be measured. The head of the femur measures 12.5 mm in diameter. The cuboid is 11.4 mm in length, and it has a small but distinct facet for articulation with the astragalus. There is a complete terminal phalanx, which is small, narrow, and fissured, with the tip set at an angle to the body of the claw.

Discussion.— *Arfia zele* differs from later species of the genus in being significantly smaller. The available sample of M_2s (6 specimens) show little overlap in size with samples of *A. shoshoniensis* or *A. opisthotoma* (Fig. 4A). The ratio of trigonid length to trigonid width in *A. zele* overlaps extensively with *A. shoshoniensis* but not with *A. opisthotoma* (Fig. 4B).

Arfia zele is known principally from the Clarks Fork Basin, but small specimens of *Arfia* described by Delson (1971) from the Powder River Basin, and by Bown (1979) from the southern Bighorn Basin probably also belong here.

Comparison of the humerus of *Arfia zele* with those of contemporary or later and slightly smaller *Prototomus phobos* suggests that *Arfia* was more heavily built than *Prototomus*.

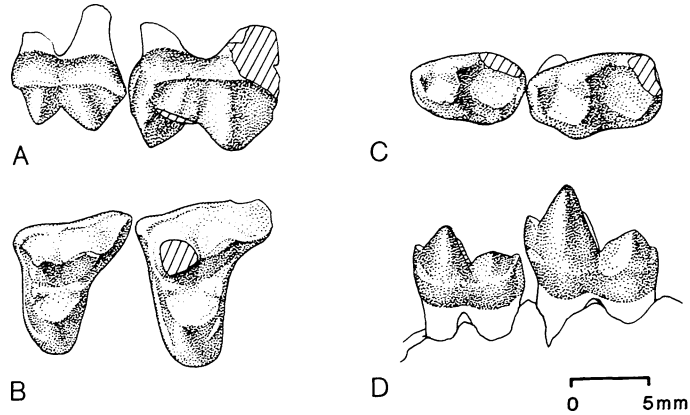

FIG. 5— Upper and lower molars of *Arfia shoshoniensis*, UM 65502 from SC-47. A and B, left M^{1-2} (M^2 reversed from right side) in lateral and occlusal view. C and D, left M_{1-2} in occlusal and lateral view. Note well separated paracone and metacone and arcuate postmetacrista on upper molars, and broadly basined talonid on lower molars.

Arfia shoshoniensis (Matthew, 1915)

Figs. 5-8

Sinopa shoshoniensis Matthew, 1915, p. 73, fig. 65.
Arfia opisthotoma (in part), Bown, 1979, fig. 52b.

Holotype.— AMNH 16158, left dentary with P_2-M_3, collected by W. Stein in 1912.

Type locality.— Five miles southeast of the mouth of Pat O'Hara Creek, Clarks Fork Basin, Wyoming (holotype is field no. 304 in AMNH Wyoming field book for 1912). This is probably UM locality SC-2 in the SE$\frac{1}{4}$, Section 26, T56N, R102W, Park County, Wyoming, or a nearby locality in the same stratigraphic interval.

Age and distribution.— Late Sandcouleean to early Graybullian, late early to early middle Wasatchian land-mammal age, early Eocene. A. *shoshoniensis* is known principally from the Clarks Fork Basin and the Bighorn Basin, Wyoming.

Diagnosis.— Resembles *Arfia zele* but differs in being about 11-17% larger in linear dimensions. Differs from *A. opisthotoma* in having a shorter, broader, less open trigonid on M_3.

Included specimens.— Foster Gulch area localities— FG-24: UM 76182 and 76189. FG-25: UM 76268. FG-29: UM 77049 and 77051. FG-30: UM 77057. FG-32: UM 77114. FG-33: UM 77139. FG-77: UM 85467 and 85470. FG-78: UM 85640. FG-83: UM 85935. FG-84: UM 86773 and 86851. FG-103: UM 87290. FG-104: UM 87330. YM-418: UM 64031. McCullough Peaks area localities— MP-23: UM 87634 and 87665. MP-24: UM 87750. MP-25: UM 87754 and 87768. MP-27: UM 87865, 87878, 87905, and 87910. Sand Coulee area localities— SC-1: UM 68164. SC-2: AMNH 16158 (holotype), and UM 72636, 72641, 80487, and 87363. SC-5: UM 64630, 83395, and 83396. SC-12: UM 64765, 64784, 69599, and 83400. SC-46: UM 66262, 67398, 77017, 83203, 83369, 86396, and 86475. SC-47: UM 65502. SC-54: UM 65789 and 75997. SC-87: UM 66233. SC-95: UM 66449. SC-96: UM 66472. SC-132: UM 71752 and 72642. SC-133: UM 72639, 72640, 75051, 79719, 82747, 82730, 82790, 83328, and 83520. SC-161: UM 68401, 68818, 72634, 75196, 79069, 80554, and 86024. SC-207: UM 69474, 69570, 80008, 82817, and 82820. SC-210: UM 72224. SC-211: 82330 and

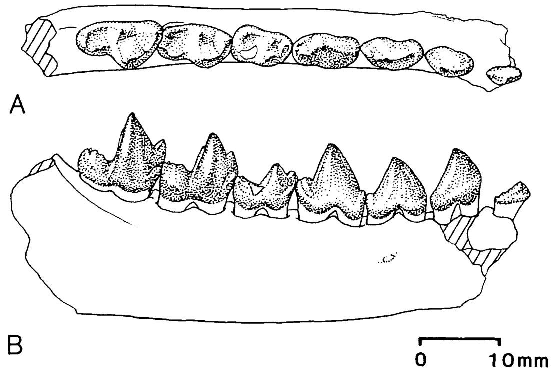

FIG. 6— Right dentary of *Arfia shoshoniensis*, UM 80487 from SC-2, with single-rooted P_1 and P_2-M_3. A, occlusal, and B, lateral view.

82339. SC-213: 69781, 69852, 75383, 79532, 81845, and 81850. SC-221: UM 83120. SC-309: UM 76554. SC-310: UM 86555. SC-311: UM 83386 and 83387. UM SC-326: SC-85544.

The following specimens from Yale-Michigan localities in the central Bighorn Basin were studied but not included in the table of measurements— YM-97: UM 63821. YM-362: UM 61768. YM-382: UM 63591. YM-389: UM 61770. YM-403: UM 63759.

Description.— Most specimens of *Arfia shoshoniensis* are fragmentary dentaries or maxillae with one or more teeth. Dentally, *A. shoshoniensis* is larger but otherwise very similar to *A. zele*. Three specimens preserve teeth in various stages of eruption. There is one incomplete rostrum. Five specimens include significant associated postcranial elements.

The three specimens with teeth erupting, UM 63591, 65502, and 72224, are all at about the same stage of development. The sequence of molar eruption is best preserved in the dentary. Relative wear indicates the universal sequence in mammals: M_1 preceded M_2, and M_2 preceded M_3. However, differences in wear on the three teeth are very slight, suggesting that the molars erupted almost simultaneously. UM 63591 has permanent P_{2-3} fully erupted in the dentary, M_3 nearly out of the crypt, and the crown of P_4 about half erupted. UM 72224 preserves both P^4 in the maxilla and M_3 in the dentary at a slightly earlier stage of eruption. Very heavy wear on M_1 seen in *Arfia*, and characteristic of Hyaenodontidae in general, must be due to concentration of bite force in this region early in adult development rather than delayed eruption of succeeding carnassial teeth (see also Mellett, 1977).

The rostrum of *A. shoshoniensis*, UM 85935, lacks incisors and canines. It is notable in showing that P^1 was double-rooted (this is also evident in UM 66449). Cheek teeth are well preserved in both maxillae. The infraorbital foramen opening above P^3 was large, measuring about 7.8 mm by 3.5 mm. The sagittal crest on the parietals was large, rising a minimum of 12 mm above the surface of the braincase. The anterior part of the zygomatic arch rises at an angle of about 45° relative to the tooth row. The latter two features indicate that the temporalis and masseter muscles of *Arfia* were large and powerful.

The lower dentition is well preserved in many specimens, although none preserve incisors. Measurable lower canines are preserved in ten specimens. These are variable in size but they do not exhibit a bimodal size distribution. There is no suggestion of sexual dimorphism in either canine size or canine shape. Seven specimens show that P_1 was consistently one-rooted. Mandibular depth can be measured in 28 specimens. Again, this measurement is variable, but there is no suggestion of bimodality or sexual dimorphism. UM 69474 includes a nearly complete right dentary measuring 133 mm from the most anterior point below alveoli for the incisors to the mandibular condyle. The ascending ramus rises 86 mm from the most anterior point, and it rises to a height of 62 mm above the base of the horizontal ramus. The condyle is cylindrical, measuring about 9 mm in diameter and 15 mm in breadth, and the articular surface wraps smoothly around the posterior half of the cylinder.

Measurements of the teeth of *A. shoshoniensis* are summarized in Table 5. Coefficients of variation of the lengths and widths of most cheek teeth are within the 4-8 range observed in modern carnivore species (Gingerich and Winkler, 1979).

The most complete associated postcranial skeleton of *Arfia shoshoniensis* is UM 69474. This specimen includes several vertebrae, the complete left humerus, the distal end of the right humerus, most of the left innominate, proximal and distal ends of the left femur, a patella, most of a left tibia, the left and right astragalus, right calcaneus, and several broken metapodials.

The humerus of UM 69474 (Fig. 7B,C) is very similar in size and general form to that of the South American bush dog *Speothos venaticus*. It measures 96.4 mm in length, and 7.8 by 12.8 mm in midshaft diameter. The proximal end, including the head, measures 24.8 mm in anteroposterior diameter, and 20.6 mm transversely across the greater and lesser tuberosities. The distal end measures 26.0 mm transversely (the distal end of the right humerus of this specimen measures 27.5 mm in breadth). The condylar surface is cylindrical, measuring 8.4 mm in diameter. The humeral head is large and set well back relative to the shaft. The shaft is moderately but distinctly curved (sigmoid) in the sagittal plane. The deltopectoral crest extends more than half the length of the shaft, and the supinator crest is present but weak. The entepicondylar foramen is well developed and there is a distinct supratrochlear vacuity. The distal end of another left humerus is preserved in UM 76554. It matches UM 69474 very closely in size and in shape (UM 76554 measures 23.9 mm in transverse breadth at the distal end and 8.1 mm in condylar diameter). The humerus of *Arfia* differs from that of a bush dog principally in retaining a more prominent entepicondyle and an entepicondylar foramen, making the distal end broader.

UM 75383 is noteworthy in preserving the proximal end of a left radius (Fig. 7F). This is oblong in outline and relatively broad, measuring 12.1 mm in breadth and only 6.9 mm in depth, with a prominent capitular eminence. The ventral surface articulating with the ulna has very little curvature, greatly limiting axial rotation of the radial shaft and precluding significant pronation and supination of the forelimb.

The innominate in UM 69474 is relatively long and narrow (Fig. 7A). It measures 127 mm in total length (including the full length of both the ilium and ischium). The sacral articulation measures about 30 mm in length and 13 mm in depth. The blade of the ilium measures about 21.8 mm in maximum depth, and the ischium measures about 14.5 mm in depth above the obturator foramen.

Preserved ends of the femur in UM 69474 (Fig. 7D,E) resemble those of a bush dog in size and in general proportions. The principal difference in *Arfia* is greater separation of the femoral head from the greater trochanter. *Arfia* resembles a racoon (*Procyon lotor*) more closely than it does a bush dog in this characteristic. Unfortunately, much of the shaft of the femur is missing, and it is impossible to estimate the total length of the femur. The femoral head is spherical, measuring 13.3 mm in maximum diameter. The proximal end of the femur measures 29.3 mm across the head and greater trochanter. The distal end of the femur measures 23.2 mm in breadth across the condyles and 24.9 mm anteroposteriorly (measured in the sagittal plane and perpendicular to the shaft). The patellar groove resembles that of *Speothos* in being higher, longer, and narrower (7.5 mm wide) by comparison with many other carnivorous mammals.

The proximal end of the tibia in UM 69474 measures 23.8 mm in breadth transversely, and about 25.7 mm anteroposteriorly. The distal end of this specimen is poorly preserved. UM 77051 includes a well preserved right distal tibia, which is distinctive in having the principal astragalar articulation strongly angled relative to the shaft, in having a distinct facet on the anterior surface of the shaft for a secondary articulation with the neck of the astragalus, and in having a distinct facet on the anterior surface of the medial malleolus for a tertiary articulation with the medial astragalar body. Both of these tibiae have astragalar articulations angled obliquely at about 45° to the tibial axis.

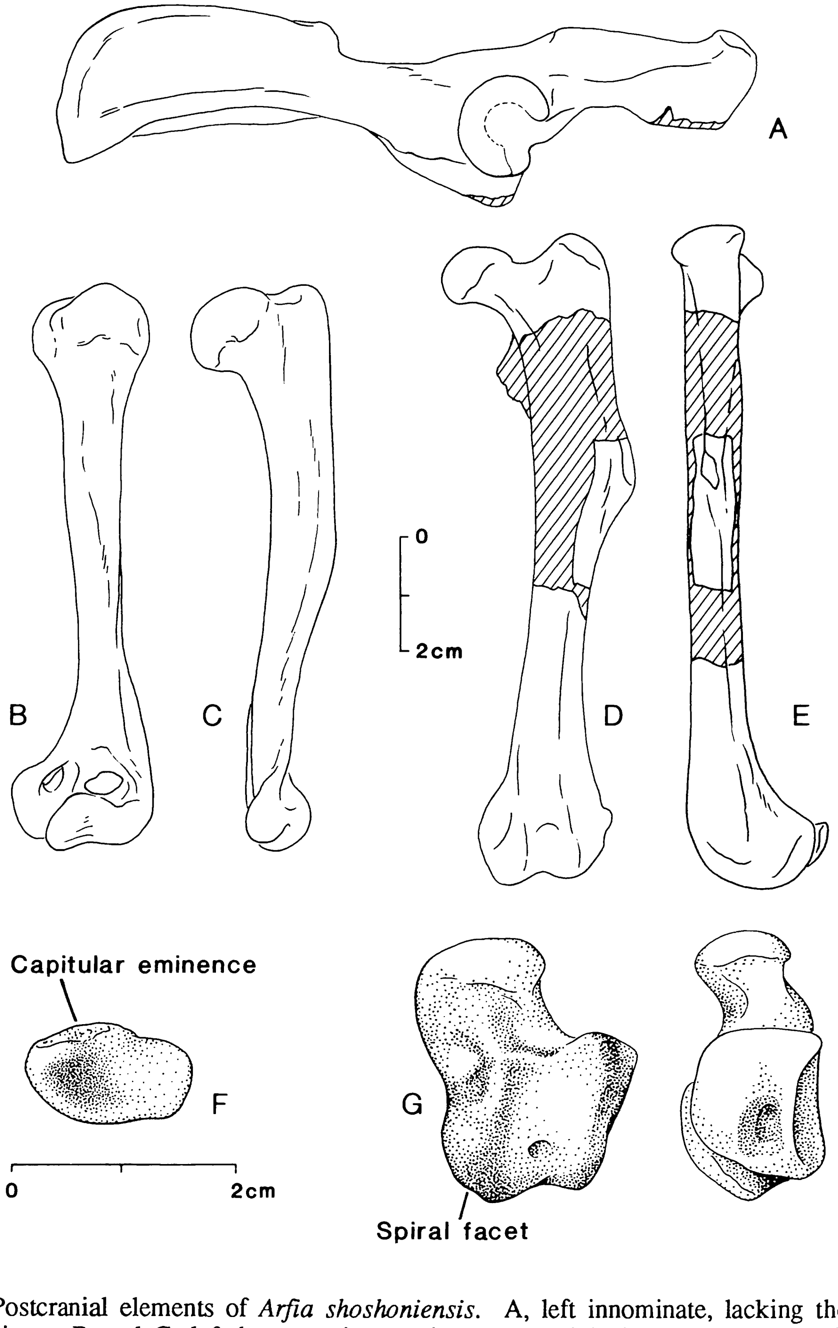

FIG. 7— Postcranial elements of *Arfia shoshoniensis*. A, left innominate, lacking the pubis, in lateral view. B and C, left humerus in anterior and medial view. D and E, left femur in anterior and medial view (length of femur restored by comparison to YPM 36932). F, right radial head in proximal view. G and H, right astragalus in dorsal and lateral view. A-E are UM 69474 from SC-207 (× 0.75). F is UM 75383 from SC-213 (× 1.5). G-H are UM 69474 from SC-207 (× 1.5). Scales are in centimeters.

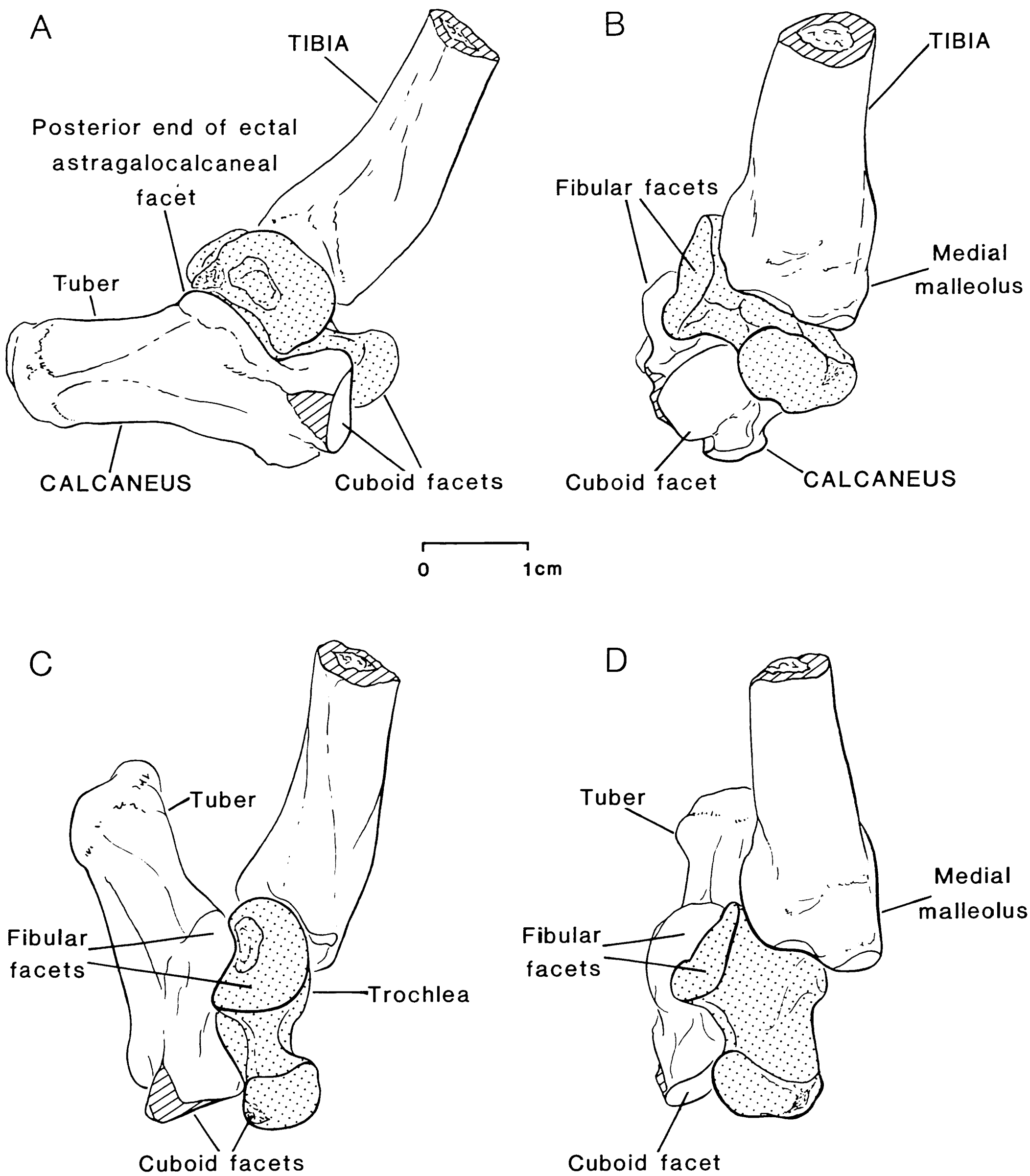

FIG. 8— Hind foot reversal in *Arfia shoshoniensis*. Right distal tibia, astragalus (shaded), and calcaneus are shown in normal dorsiflexed everted posture (A and B) and in plantarflexed inverted posture (C and D). Hind foot reversal here results from extreme plantarflexion at the tibioastragalar joint and simultaneous inversion at the astragalocalcaneal joint. Note how the calcaneus moves from a normal position lateral to the astragalar head to a more ventral position during extreme plantarflexion. Supination at the transverse tarsal joint, comprising the astragalonavicular and calcaneocuboid articulations, probably enhanced hind foot reversal as well. Distal midshaft and medial malleolus of some tibiae (including that shown here) preserve distinct facets for articulation with the neck and medial shelf of the astragalus. Calcanei and astragali of *Arfia* both exhibit substantial facets for articulation with the fibula and cuboid. A and C, lateral view. B and D, anterior view. Distal tibia is part of UM 77051, and astragalus and calcaneous are part of UM 87768.

UM 69474 includes associated astragali (e.g., Fig. 7G,H) and a right calcaneus, and a right astragalus and calcaneus are also associated in UM 87768. The right astragalus of UM 69474 measures 19.8 mm in total length, 9.4 mm across the trochlea, and 12.5 mm across the full body, and the head measures 10.9 mm in width and 7.0 mm in depth. The right astragalus of UM 87768 measures 20.1 mm in total length, 10.4 mm across the trochlea, and 13.9 mm across the full body, and the head measures 11.6 mm in width and 7.4 mm in depth. There is a distinct astragalar foramen perforating the body in all specimens, the trochlea is shallow, and there is a broad shelf of bone on the dorsal surface of the body medial to the trochlea. The shelf has a distinct facet for articulation with the medial malleolus of the tibia in UM 69474, but there is no trace of this facet in UM 87768. There is a distinct spiral facet on the posteromedial surface of the astragalar body, facilitating hind foot reversal (see discussion). There is also a small but distinct facet for articulation with the cuboid on the ventral surface of the astragalar head.

The calcaneus in UM 69474 measures 36.3 mm in total length, with the calcaneal tuber accounting for 16.0 mm of this (measured from the posterior end of the ectal astragalocalcaneal facet). The calcaneus in UM 87768 measures 33.6 mm in total length, with the calcaneal tuber accounting for 17.8 mm of this. The calcaneal tuber angles downward at an angle of about 20-30° relative to the body of the calcaneus. The facet for articulation with the fibula is relatively large, forming a convex curving ridge along the lateral side of the ectal facet. The cuboid facet is large and triangular in UM 69474. It is more nearly square in UM 87768, measuring about 7.8 mm on a side. The sustentacular process is relatively broad in UM 69474, measuring 6.2 mm in diameter parallel to the calcaneal axis and 8.2 mm perpendicular to this axis.

Discussion.— *Arfia shoshoniensis* is clearly larger than *A. zele* (Fig. 4A). Matthew distinguished "*Sinopa*" *shoshoniensis* from "*Sinopa*" *opisthotoma* by its "typical proportions of the molar shears" (Matthew, 1915, p. 74), and this difference is evident when measured quantitatively (Tables 5 and 6, Figure 4B).

Postcranial remains associated with UM 69474 and 87768 provide new information about the body size and locomotor habits of *Arfia*. Close similarity of preserved elements to those of extant *Speothos* suggest that *Arfia* probably weighed about 5-7 kg, and that it was a stoutly built cursorial predator.

The distal tibia of UM 77051 can be articulated with the astragalus of UM 87768, and this astragalus can be articulated in turn with the associated calcaneus. Manipulation of these elements indicates that the foot was habitually somewhat dorsiflexed (Fig. 8A,B), and that there was a narrow range (about 35°) of normal sagittal dorsiflexion-plantarflexion of the foot relative to the tibia. Habitual dorsiflexion and the narrow range of tibioastragalar flexion, together with downward angulation of the calcaneal tuber, suggests that *Arfia* was habitually plantigrade. Angulation of the tibiotarsal joint means that the foot was somewhat everted relative to the tibia when dorsiflexed, but this eversion gave way to inversion during plantarflexion (Fig. 8C,D).

Inversion with plantarflexion is clear in the tibioastragalar joint of the ankle. Manipulation indicates that there was some potential for inversion and eversion of the pes at the astragalocalcaneal joint as well. Movement at the transverse tarsal joint cannot be evaluated at present. However, the principal spiral tibioastragalar mechanism of hind foot reversal in *Arfia* appears to have been more similar functionally to that in *Didelphis* than to the complex three-joint mechanism characteristic of most other eutherians studied to date (Jenkins and McClearn, 1984). (The spiral tibioastragalar mechanism of *Arfia* differs in detail from that of *Didelphis*, and it certainly evolved independently.)

Inversion with plantarflexion permits an unusual degree of hind foot reversal, which is characteristic of arboreal species descending trees head first. If *Arfia* was a *Speothos*-like cursor, it differed in being plantigrade and it differed in having an ankle very different from that of most cursors. Ability to reverse the hind foot suggests that *Arfia* was at least partly arboreal.

Ability to invert the foot at the tibioastragalar joint during plantarflexion is associated with a foot structure different from that of Bridgerian *Sinopa* (Matthew, 1906), extending Van Valen's (1965) separation of these genera based on teeth.

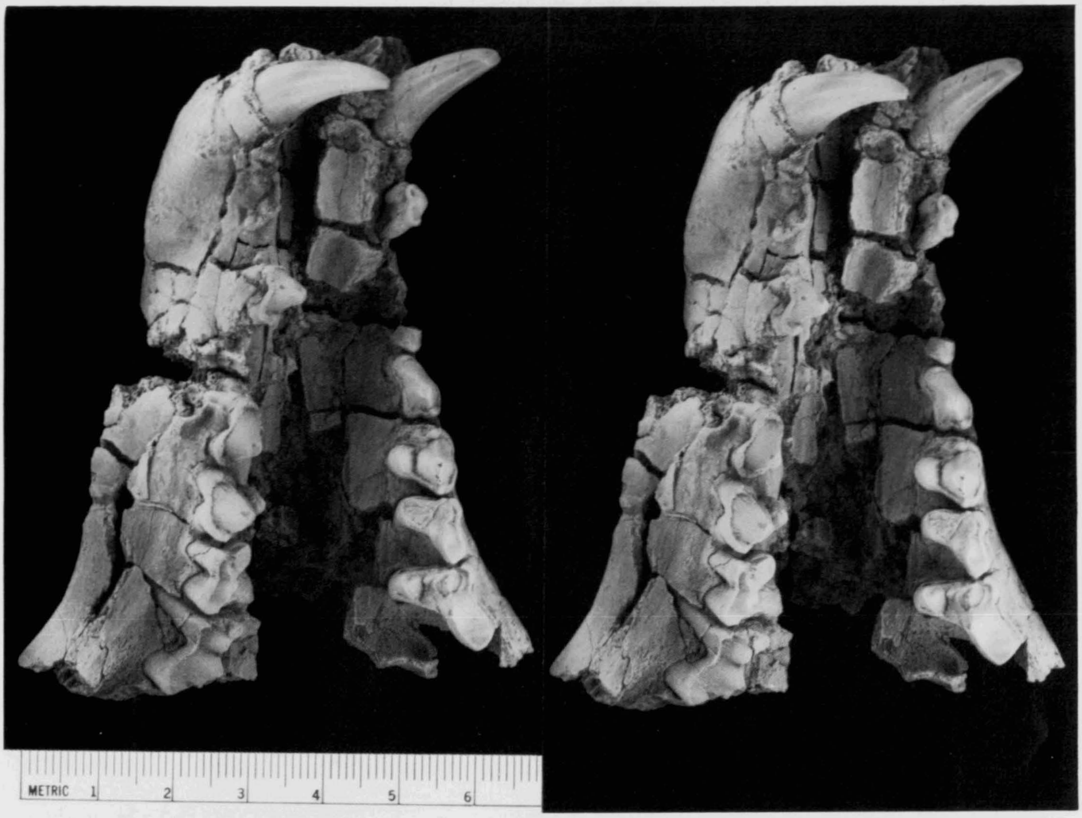

FIG. 9— Rostrum of *Arfia opisthotoma*, UA 8271 from McCullough Peaks area of Bighorn Basin, Wyoming. Specimen preserves intact crowns of left C^1, P^1, P^3-M^2, and right C^1, P^2, P^3-M^2. Stereophotograph, occlusal view.

Arfia opisthotoma (Matthew, 1901)
Figs. 9-10

Stypolophus sp., Osborn and Wortman, 1892, p. 110.
Sinopa opisthotoma Matthew, 1901, p. 28, fig. 9.

Holotype.— AMNH 99, upper and lower jaws.

Type locality.— Bighorn Basin, Wyoming.

Age and distribution.— Graybullian, middle early Wasatchian land-mammal age, early Eocene. *A. opisthotoma* is known primarily the Clarks Fork Basin and Bighorn Basin, Wyoming.

Diagnosis.— *A. opisthotoma* is similar in size to *A. shoshoniensis*, but differs from earlier species of *Arfia* in having a longer, narrower, more open trigonid on M_3.

Included specimens.— Foster Gulch area localities— FG-87: UM 86827. McCullough Peaks area— UA 8271. Sand Coulee area localities— SC-32: UM 82956 and 82965. SC-34: UM 65303, 71531, 72644, 73929, 78996, and 79001. SC-35: UM 73947 and 73952. SC-36: UM 66773 and 71699. SC-63: UM 65728. SC-64: UM 72638. SC-128: UM 67047, 67159, 69949, 76699, 76717, 79164, 79168, 79180, 79182, and 79189. SC-192: UM 68899, 69131, 69162, 69612, 69619, 79239, 79248, 79260, 79290, and 82898. SC-225: UM 72643. SC-237: UM 83072. SC-265: UM 73466. SC-354: UM 88094.

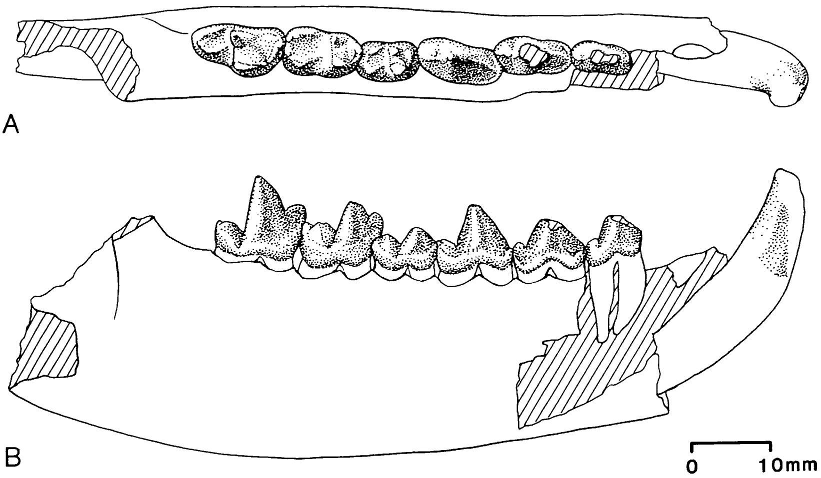

FIG. 10— Right dentary of *Arfia opisthotoma*, UM 69949 from SC-128, with C_1 and P_2-M_3. A, occlusal, and B, lateral view. Drawing is composite based on both left and right dentaries preserved in this specimen.

Description.— *Arfia opisthotoma* is less well known than *A. shoshoniensis*. The most complete upper dentition is part of the rostrum, UA 8271 (Fig. 9), and the most complete lower dentition is UM 69949 (Fig. 10). There are no postcranial remains.

UA 8271 has both upper canines in place. These are high-crowned pointed teeth, but they do not have sharp anterior or posterior edges. P^1 is double-rooted. $P^{2\text{-}3}$ are also double-rooted, with a large apical cusp and a smaller posterior basal cusp. P^4 is three-rooted and has a distinct lingual protocone in addition to its labial apical and basal cusps. The molars have the paracone and metacone well separated, a large protocone, and the continuous postmetacrista characteristic of *Arfia*. Alveoli remain for M^3 but the crowns are missing on both sides. A frontal fragment with this specimen preserves impressions of the olfactory bulbs of the brain and the bases of several ethmoturbinal scrolls.

UM 69949 is a left dentary with C_1, alveoli for a single-rooted P_1, double-rooted $P_{2\text{-}3}$, intact crowns of P_4 and $M_{1\text{-}3}$, and a right dentary with intact crowns of P_2-M_3.

Measurements of the teeth of *Arfia opisthotoma* are summarized in Table 6. Coefficients of variation of the lengths and widths of most cheek teeth are within the 4-8 range observed in modern carnivore species (Gingerich and Winkler, 1979).

Discussion.— *Arfia opisthotoma* is very similar to *A. shoshoniensis*, but quantitative comparison (Tables 5 and 6, Fig. 4B) shows that *A. opisthotoma* has a slightly longer, narrower M_3 trigonid than *A. shoshoniensis*. Given a representative sample, this difference is sufficient to distinguish the two and Matthew (1915) now appears to be justified in having separated them.

Prototomus Cope, 1874

Type species.— *Prototomus viverrinus* Cope, 1874.

Included species.— *Prototomus deimos*, new species; *P. phobos*, new species; *P. martis*, new species; *P. viverrinus* Cope, 1874; *P. secundarius* Cope, 1875; *P. robustus* (Matthew, 1915); and questionably *P.? vulpeculus* (Matthew, 1915).

Age and distribution.— Wasatchian land-mammal age, early Eocene, of western North America.

Diagnosis.— *Prototomus* differs from European *Proviverra* in having narrower, more sectorial talonids on lower molars, with the cristid obliqua angled toward the metaconid rather than the protoconid. *Prototomus* differs from North American *Tritemnodon*, which it otherwise resembles, in having an anteroposteriorly short, broad, "closed," trigonid on lower molars, especially M_3 and in retaining a single-rooted P_1. Differs from most genera of proviverrines in having an elongated anterior dentary with anterior premolars separated by diastemata. Other differences are summarized in the key in Figure 27.

Discussion.— *Prototomus* was the first early Eocene hyaenodontid described from North America. As outlined above, *Prototomus* is based on a species that is based on an indeterminate type specimen that is now lost. The name is here applied to the most common and diverse group of early and middle Wasatchian hyaenodontid species (1) because this group lacks any other generic name, and (2) because commonness and diversity makes it most likely that this is the group of species first sampled by Cope.

Van Valen (1965) included two European species, *P. palaeonictides* (Lemoine, 1880) and *P. torvidus* Van Valen, 1965, in *Prototomus*. The type (MNHN Al-5515) and referred specimens (e.g., Rich, 1971) of the former species have broad talonids with substantial entoconids on M_{1-2}, which are characteristic of European *Proviverra* Rütimeyer, 1862, but unlike *Prototomus*. Consequently, *P. palaeonictides* is here referred to *Proviverra*. Lange-Badré (1984) placed Van Valen's species *P. torvidus* in a new genus *Hurzelerius*. Consequently *Prototomus* is no longer represented in Europe.

Species of *Prototomus* are so similar to each other that overall size and the pattern of change of size over time appear to be the only characteristics distinguishing them. Individual species of *Prototomus* have the variability characteristic of species of mammals living today (see tables). Clustering of specimens about a mean size well separated from another contemporary cluster (or clusters) indicates that two or sometimes three species are present in samples from most stratigraphic intervals. Tracing these clusters through time (e.g., Fig. 19) indicates that clusters representing small, medium, and large species in the middle and late Wasatchian are probably derived from clusters representing medium and medium-to-large species in the early Wasatchian. This interpretation could not be derived from the morphology of available specimens alone, and it remains a hypothesis to be tested by discovery of new material.

Prototomus deimos, new species

Fig. 11

Cf. *Tritemnodon* sp. (in part), Bown, 1979, p. 89.
Prolimnocyon atavus (in part), Bown, 1979, p. 90.

Holotype.— UM 79612, left dentary with crowns of P_1 and M_{2-3}, and right dentary with crowns of P_2 and P_4-M_3, collected by William J. Ryan.

Type locality.— University of Michigan locality SC-213 in the Clarks Fork Basin: N$\frac{1}{2}$, Section 26, T56N, R101W, Park County, Wyoming.

Age and distribution.— Sandcouleean and early Graybullian subages of Wasatchian land-mammal age, early part of the early Eocene, Bighorn and Clarks Fork basins, Wyoming.

Diagnosis.— Smallest species of *Prototomus*.

Etymology.— Named for Deimos, smaller and more distant of two satellites of the planet Mars.

Included specimens.— Foster Gulch area locality— FG-20: UM 76142. Sand Coulee area localities— SC-4: UM 64645. SC-44: UM 76469. SC-87: UM 66260. SC-213: UM 69800, 79602, and 79612 (holotype). SC-310: UM 84769.

Description.— The only maxilla of *P. deimos* is UM 64646, which is badly broken. UM 79602 is an isolated M^1 preserving the confluent paracone and metacone of generalized

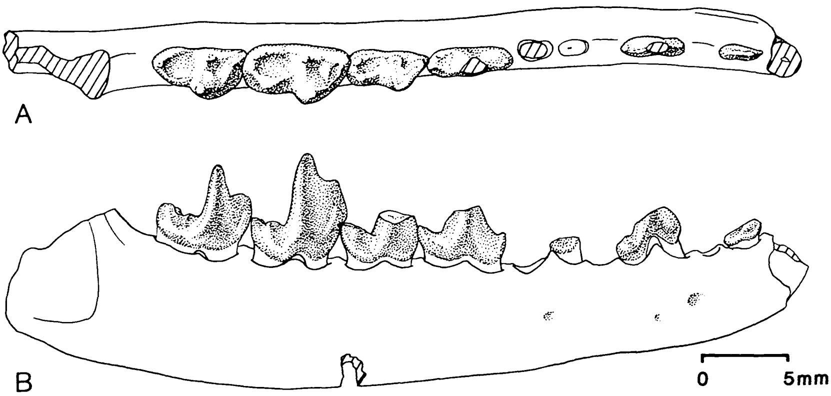

FIG. 11— Right dentary of *Prototomus deimos*, UM 79612 (holotype) from SC-213, with root of C_1, single-rooted P_1, double-rooted P_2, and P_4-M_3. A, occlusal, and B, lateral view. M_{2-3} partially restored from associated left dentary.

hyaenodontids. The protocone is prominent, flanked by a distinct paraconule and slightly lower metaconule. The postmetacrista is well developed and distinctly notched.

Three dentaries preserve alveoli for a single-rooted P_1, and the crown of this tooth is preserved in the holotype. It is very low and narrow. Double-rooted P_{2-4} have crowns that are relatively low, long, and narrow as well. There is no trace of a metaconid on any of the lower premolars. All three of these premolars have a narrow sectorial talonid with a small but distinct hypoconid (best developed on the more posterior teeth). Moderate diastemata separate P_2 from P_1 and P_3 from P_2. Molar trigonids are moderately closed, with the protocone, paracone, and metacone approximately equidistant from each other. The talonids are basined, but rather narrow and angled labially relative to their respective trigonids. The hypoconid is larger than the entoconid, and the lingual side of the talonid is curved rather than straight.

Measurements of the holotype of *Prototomus deimos* are given in Table 7, and a statistical summary of dental measurements for the species is given in Table 8. Coefficients of variation of the lengths and widths of most cheek teeth are within the 4-8 range observed in modern carnivore species (Gingerich and Winkler, 1979).

Discussion.— This species is very similar to, but smaller than, its contemporary *Prototomus phobos*. It has not been found higher than the 1760 meter interval in the Clarks Fork Basin, but this may reflect its rarity rather than its extinction at the level. Higher levels are not as well sampled.

Two specimens, UW 9816 and 9903, that Bown (1979) referred to *Prolimnocyon* and *Tritemnodon*, respectively, probably belong here.

Prototomus phobos, new species

Figs. 12, 13, 20C,D

Sinopa cf. *S. viverrina*, Jepsen, 1930, p. 118.
Prototomus sp. (in part), Bown, 1979, p. 88.
Tritemnodon sp. (in part), Bown, 1979, p. 89, fig. 52d.

Holotype.— YPM-PU 13019, skull and lower jaws preserving most of the dentition.

Type locality.— "*Omorhamphus*" locality of Sinclair (1928), stated by Jepsen (1930) to be "about one and one-half miles southeast of Dorsey Creek and perhaps two miles south of the old Otto-Basin road," which must be in or near the southwest corner of T51N, R94E, Big Horn County, Wyoming.

FIG. 12— Skull and dentary of *Prototomus phobos*, YPM-PU 13019 (holotype) from south of Dorsey Creek in the central Bighorn Basin, in right lateral view. Specimen preserves left I^{1-2}, double-rooted P^{1-2}, and P^4-M^3, right P^3-M^3, left C_1 and P_2-M_3, and right P_1-M_3.

Age and distribution.— *Prototomus phobos* is known from the Sandcouleean through middle Graybullian subages of the Wasatchian land-mammal age, early Eocene It is known principally from the Bighorn and Clarks Fork basins, Wyoming.

Diagnosis.— Differs from *P. deimos* in being three to four normalized standard deviations larger. Differs from *P. martis* in being two to three normalized standard deviations smaller, on average, although *P. phobos* and early *P. martis* are difficult to distinguish. Differs from *P. viverrinus* in being larger and from *P. secundarius* in being smaller, and differs from both of these later species in having slightly longer, narrower, and less basined talonids on lower molars. Differs from *P. robustus* in being four to five normalized standard deviations smaller on average.

Etymology.— Named for Phobos, larger and closer of two satellites of the planet Mars.

Included specimens.— Foster Gulch area localities— FG-20: UM 76137. FG-25: UM 76261. FG-42: UM 77210. FG-60: UM 85347. McCullough Peaks area locality— MP-122: UM 92576, 92614, and 92640. Sand Coulee area localities— SC-1: UM 81966. SC-2: UM 80504. SC-16: UM 76306. SC-17: UM 73749. SC-26: UM 72637. SC-26: UM 74044. SC-37: UM 69408 and 69441. SC-43: UM 65435. SC-64: UM 74134. SC-128: UM 67037. SC-133: UM 68075 and 82711. SC-161: UM 68326, 68677, 68704, 72631, 72632, 72633, 77471, 77522, 79124, and 80518. SC-192: UM 79256, 79261, 82910, and 85716. SC-210: UM 72163 and 72214. SC-211: UM 82321. SC-213: UM 75393 and 84660. SC-225: UM 71224. SC-253: UM 74524. SC-303: UM 75723. SC-304: UM 75744. SC-323: UM 79358. SC-353: UM 88076. Yale-Michigan localities in the central Bighorn Basin— YM-357: UM 63858. YM-431: UM 64365.

The following specimens described by Bown (1979) probably belong here: UW 9777, 9779, 9785, 9796, 9798, 9805, 9809, 9818, 9835, 9846, 9880, 9895, 9905, 9941. These span the 27-119 meter interval in Bown's stratigraphic section.

Description.— *Prototomus phobos* is the best known species of the genus dentally and cranially. The holotype, YPM-PU 13019, includes a laterally compressed but nearly complete cranium measuring ca. 97 mm in length (Fig. 12). It is smaller but otherwise similar to the cranium of *Sinopa* described and illustrated by Matthew (1906). The infraorbital foramen measures 3.6 mm in depth and 1.3 mm in width. The orbit measures approximately 11 mm in diameter. The basicranium is badly crushed and nothing can be determined about its form without considerable reconstructive preparation.

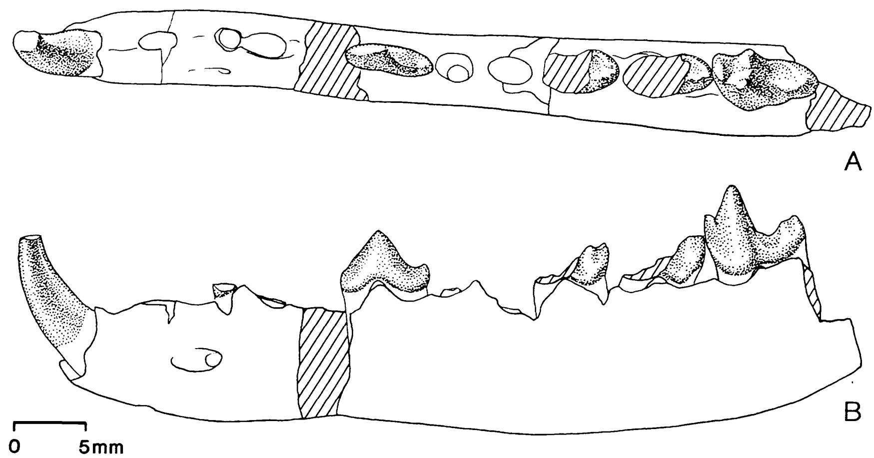

FIG. 13— Left dentary of *Prototomus phobos*, UM 68075 from SC-133, with C_1, P_3, and M_{1-3}. A, occlusal, and B, lateral view.

The upper dentition is well preserved in the holotype. Crowns of I^{1-2} are preserved. These are closely appressed at the midline of the skull. Both are slightly worn, but both appear to have had a central cusp flanked by medial and lateral cuspules like the upper incisors of *Arfia zele* described above. An alveolus is present for I^3 next to that housing I^2, and this is flanked laterally by a deep groove in the premaxilla that received the crown of the lower canine when the mouth was closed. The upper canine is not preserved. P^1 is double-rooted, with a long, narrow, low crown. Crowns of P^2 and P^3 are higher and more pointed, but they are also long and narrow. Both have a small posterior cusp and P^3 has a slight internal swelling, but neither has any trace of a protocone. P^4 has a large pointed labial cusp, with a well developed posterior accessory cusp connected by a distinctly notched crest. There is a large lingual shelf on P^4, but no real protocone cusp. The molars have connate paracones and metacones, and a distinct lingual protocone with a small paraconule and smaller metaconule. M^{1-2} have a distinctly notched postmetacrista, but the metacone is reduced on M^3 and there is no postmetacrista. A detailed drawing of upper molars of this species is included in Figure 20.

The holotype preserves the most complete dentaries. These are long and slender, with a high ascending ramus and shallow masseteric fossa. The condyle is low, broad, and cylindrical, and the angle is distinctly hooked. There is a short diastema between C_1 and P_1, and longer diastemata separating P_1 from P_2, and P_2 from P_3. A very short space separates P_3 from P_4. There are mental foramina beneath the P_1-P_2 diastema and beneath the anterior root of P_3.

The holotype, YPM-PU 13019, preserves a single incisor alveolus, but there were undoubtedly three small incisors in life. The crown of the lower canine is slender and closely positioned near the midline, as is typical of carnivorous mammals. P_1 is single-rooted with a low, narrow, forwardly-inclined crown. Three other specimens of this species preserve alveoli for single-rooted P_1s. P_{2-4} are double-rooted and increase progressively in size and development of accessory cuspules posteriorly. On P_4 there is a small anterior cuspule and a distinct posterior cusp connected to the protoconid by a notched crest. The protoconid, paraconid, and metaconid are approximately equidistant on M_1, but the paraconid and metaconid are closer together on M_2 and M_3, making a relatively closed trigonid. The talonids on M_{1-2} are moderately broad and slightly basined. The talonid on M_3 is narrower. The hypoconid is distinctly larger than the entoconid on M_2 and M_3. Both have a distinct hypoconulid as well. The dentition of a referred dentary is illustrated in Figure 13.

Measurements of the holotype of *Prototomus phobos* are given in Table 9, and a statistical summary of dental measurements for the species is given in Table 10. Coefficients of variation of the lengths and widths of most cheek teeth are within the 4-8 range observed in modern carnivore species (Gingerich and Winkler, 1979).

Discussion.— *Prototomus phobos* is difficult to distinguish from the slightly larger *P. martis*, requiring that a reasonable sample, preferably in stratigraphic context, be available for identification.

Prototomus martis, new species

Figs. 14, 15

Tritemnodon sp. (in part), Bown, 1979, p. 89, fig. 52c?
Prolimnocyon atavus (in part), Bown, 1979, p. 90.

Holotype.— UM 87317, left dentary with alveoli for C_1-P_4 and crowns of M_{1-3} (pt.), and right dentary with broken C_1, alveoli for P_{2-3}, and crowns or partial crowns of P_4-M_3, collected by Gregg F. Gunnell.

Type locality.— University of Michigan locality FG-103 in the northern Bighorn Basin: NW$\frac{1}{4}$, Section 32, T53N, R95W, Big Horn County, Wyoming.

Age and distribution.— *Prototomus martis* is known from the late Sandcouleean through early Graybullian subages of the Wasatchian land-mammal age, early Eocene, and it is known with certainty only from the Bighorn and Clarks Fork basins, Wyoming.

Diagnosis.— Largest Sandcouleean and early Graybullian species of *Prototomus*. Clearly distinguished from contemporary *P. deimos* and later *P. viverrinus* by its larger size. Differs from *P. viverrinus* and from *P. secundarius* in having slightly longer, narrower, and less basined talonids on lower molars. Similar to earlier, possibly ancestral, and contemporary *P. phobos*, but differs in being two to three normalized standard deviations larger, on average. Differs from its putative descendant *P. robustus* in averaging one to two normalized standard deviations smaller. Differs from type and at least one referred specimen of *P. robustus* in retaining a relatively large M_3.

Etymology.— Named for Mars, god of war in Roman mythology, in allusion to the predatory habits of this large *Prototomus*.

Included specimens.— Foster Gulch area localities— FG-23: UM 76174.
FG-24: UM 76187. FG-94: UM 87144. FG-103: UM 87317. Graybull River area locality in the central Bighorn Basin— GR-18: UM 87228. McCullough Peaks area localities— MP-23: UM 87664. MP-138: UM 93270. MP-148: UM 93598. MP-165: UM 94036. Sand Coulee area localities— SC-2: UM 78925, 85842, and 87356. SC-12: UM 69598. SC-46: UM 86399. SC-47: UM 65470 and 86498. SC-54: UM 82239. SC-87: UM 68544 and 79817. SC-88: UM 86205. SC-95: UM 76646. SC-114: UM 74523. SC-133: UM 67138, 68067, and 79745. SC-192: UM 69186. SC-207: UM 69559 and 69571. SC-213: UM 69812, 71100, 79572, 81846 and 82138. SC-318: UM 77374. Yale-Michigan localities in the central Bighorn Basin— YM-387: UM 63649. YM-410: UM 63906.

The following specimens described by Bown (1979) probably belong here: UW 9818, 9833, and 9865. These span the 113-180 meter interval in Bown's measured stratigraphic section.

Description.— One deformed skull of *Prototomus martis* is known, UM 69559, but this is somewhat crushed and it adds no new information beyond what is evident in YPM-PU 13019, holotype of *P. phobos*. Cranially and dentally, *P. martis* is very similar to *P. phobos* and it appears to differ only in being larger. UM 69559 shows P^1 to have been double-rooted. P_1 is consistently single-rooted in eight dentaries preserving this tooth or its alveolus.

Dental measurements of the holotype of *Prototomus martis* are given in Table 11, and a statistical summary of dental measurements for the species is given in Table 12. Coefficients of variation of the lengths and widths of most cheek teeth are within the 4-8 range observed in modern carnivore species (Gingerich and Winkler, 1979).

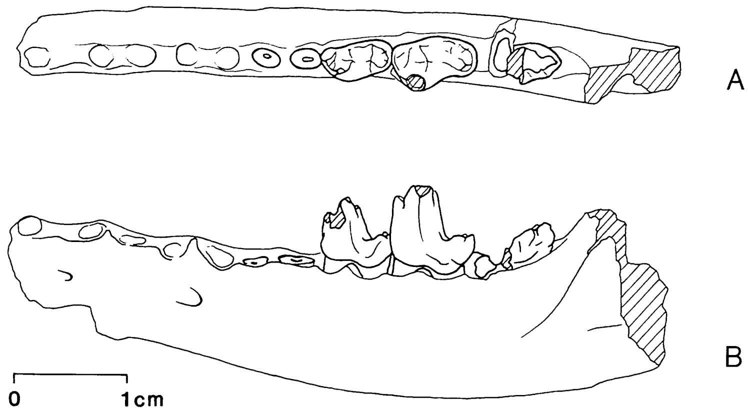

FIG. 14— Left dentary of *Prototomus martis*, UM 87317 (holotype) from FG-103, with $M_{1\text{-}3}$. A, occlusal, and B, lateral view.

Prototomus martis is the only early Wasatchian species with significant associated postcranial remains. UM 63906 preserves the distal end of a right scapula, the proximal end of a right radius, and the proximal two-thirds of a left femur. UM 87356 preserves a nearly complete left femur, the right astragalus, and the left cuboid. UM 93598 preserves the distal end of a right scapula, complete right humerus, proximal two-thirds of the right ulna, and distal half of the right radius.

The scapula has an ovoid glenoid cavity, with a prominent tuberosity and coracoid process (Fig. 15A), and the remnant of a high scapular spine. The humerus resembles that of *Arfia* described above, but it is relatively longer and less heavily built (Fig. 15B,C). It measures 80.8 mm in length, and 6.6 by 10.8 mm in midshaft diameter. The proximal end, including the head, measures 14.3 mm in anteroposterior diameter, and 14.9 mm transversely across the greater and lesser tuberosities. The distal end measures 21.6 mm transversely. The condylar surface is cylindrical, measuring approximately 6.0 mm in diameter. As in *Arfia*, the humeral head is large and set well back relative to the shaft. The shaft is straighter than that in *Arfia*. As in *Arfia*, the deltopectoral crest extends more than half the length of the shaft, and the supinator crest is present but weak. The entepicondylar foramen is well developed, and there is a distinct supratrochlear vacuity but this is much smaller than that of *Arfia*.

The ulna is 68.8 mm in length as preserved, but this is not the complete length, so its functional proportions cannot be determined. The ulna appears to be bowed dorsally at midshaft, but it was reconstructed from numerous pieces and this curvature may be distorted. The olecranon of the ulna extends 13.5 mm beyond the anconeal process. The radial head is oblong in outline and relatively broad (Fig. 15F), measuring 8.5 mm in breadth and 5.8 mm in depth, with a prominent capitular eminence. As in *Arfia*, the ventral surface of the radial head articulating with the ulna has little curvature, greatly limiting axial rotation of the radial shaft and limiting pronation and supination of the forelimb. The distal radius (Fig. 15G) has a distinct ulnar facet, a well marked groove for the common digital extensor tendon, and a prominent styloid process, and the carpal articular surface is nearly as deep anteroposteriorly as it is broad mediolaterally.

The femur in UM 87356 measures 87.3 mm in length (Fig. 15D,E). It has a spherical head measuring 9.4 mm in diameter. The corresponding measurement in UM 63906 is 10.2 mm. Proximal ends of the two femora measure 22.8 and 19.0 mm across the head and greater trochanter. Midshaft diameters are 6.2 × 8.6 and 6.3 × 8.4, respectively. UM 87356 measures 17.8 mm across the two condyles and 16.0 mm anteroposteriorly (measured in the sagittal plane and perpendicular to the shaft). As in *Arfia*, the patellar groove is higher, longer, and narrower (5.8 mm wide) by comparison with many other carnivorous mammals.

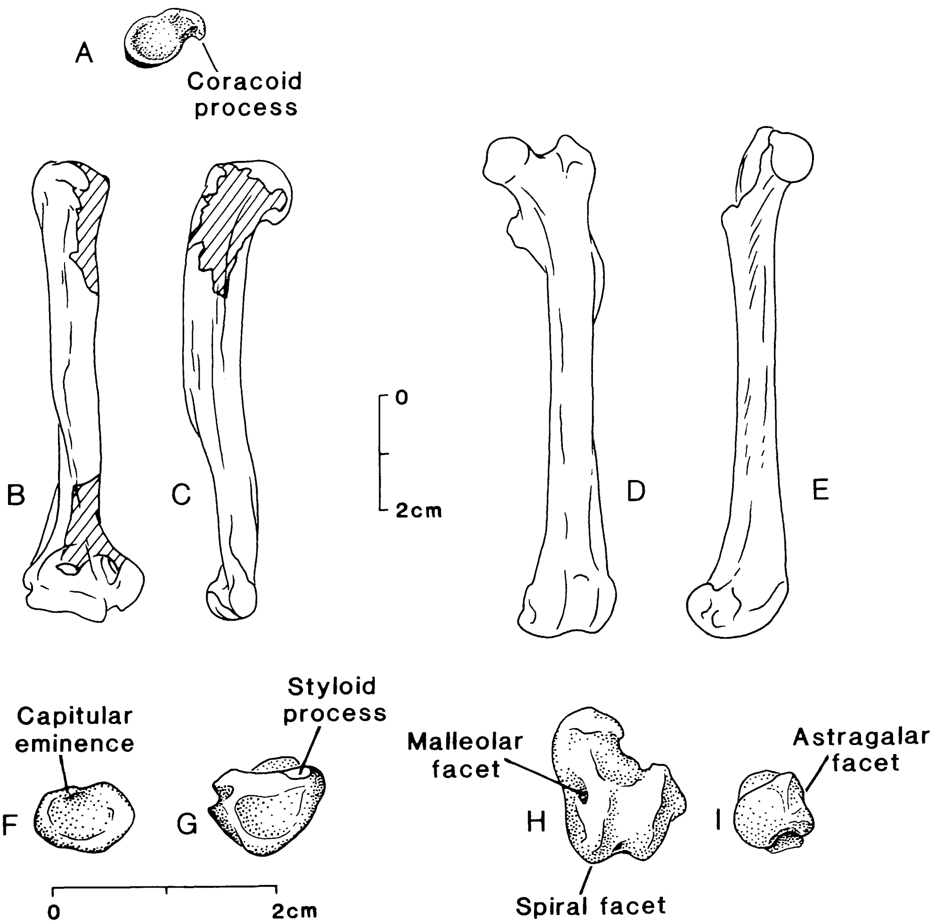

FIG. 15— Postcranial elements of *Prototomus martis*. A, glenoid of right scapula, in articular view. B and C, right humerus in anterior and medial view. D and E, left femur in anterior and medial view. F, proximal end of right radius. G, distal end of right radius. H, right astragalus in dorsal view. I, proximal end of left cuboid. A-C are UM 93598 from MP-148 (× 0.75). D and E are UM 87356 from SC-2 (× 0.75). F is UM 63906 from YM-410 (× 1.5). G is UM 93598 (× 1.5). H and I are UM 87356 (× 1.5). Scales are in centimeters.

The astragalus of *Prototomus* (Fig. 15H) is smaller, but otherwise closely resembles that of *Arfia*. It measures 14.1 mm in total length, 7.2 mm across the trochlea, and 9.5 mm across the full body. The head measures 6.7 mm in width and 4.0 mm in depth. There is a very small but distinct astragalar foramen perforating the body, the trochlea is shallow, and there is a broad shelf of bone on the dorsal surface of the body medial to the trochlea. This shelf has a distinct facet for articulation with the medial malleolus of the tibia. As in *Arfia*, there is a distinct spiral facet on the posteromedial surface of the astragalar body, facilitating hind foot reversal. The ventral surface of the astragalar head is poorly preserved, and the cuboid articulation is obliterated. The cuboid measures 9.1 mm in length, 6.7 mm in width, and 6.5 mm in depth, and it is noteworthy chiefly in preserving a distinct articulation for the astragalus as well as the calcaneus (Fig. 15I).

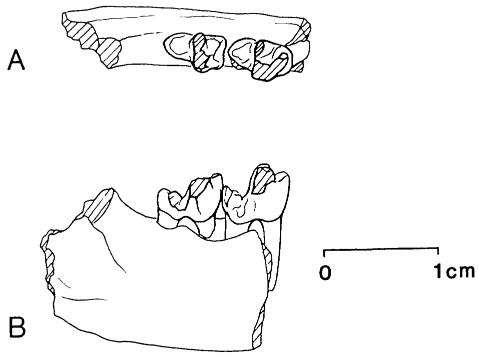

FIG. 16— Right dentary of *Prototomus viverrinus*, UM 64178 from YM-421, with $M_{2\text{-}3}$. A, occlusal, and B, lateral view.

Discussion.— *Prototomus martis* is sufficiently similar to its partially contemporary congener *P. phobos* that some individual specimens, particularly those preserving only upper cheek teeth, probably cannot be assigned reliably to one species or the other. This is reflected in extensive overlap of dental measurements in Tables 10 and 12.

Teeth and postcranial bones indicate that *Prototomus martis* was smaller than *Arfia shoshoniensis*. To judge from comparison of limb elements, *P. martis* probably weighed 1.5 to 2.0 kg. Comparison with *Arfia* suggests that *Prototomus* too was probably a cursorial predator, but lighter in weight and a little more gracile in build. Hind foot reversal indicates that *Prototomus*, like *Arfia*, was at least partly arboreal.

Prototomus viverrinus Cope, 1874

Fig. 16

Prototomus viverrinus Cope, 1874, p. 13; 1875, p. 9.
Stypolophus viverrinus, Cope, 1877, p. 112, Pl. 38:1-11.
Sinopa viverrina, Matthew, 1901, p. 27; 1915, p. 83.

Holotype.— USNM 1022, palate (now lost) and fragments of skeleton questionably associated.

Type locality.— San Jose Formation of San Juan Basin, New Mexico.

Age and distribution.— *Prototomus viverrinus* is known from the middle to late Wasatchian of the San Juan Basin, New Mexico, and the Bighorn Basin, Wyoming.

Diagnosis.— Smallest of the middle to late Wasatchian species. Differs from earlier species of the genus in having slightly shorter, broader, and more basined talonids on lower molars.

Included specimens.— Yale-Michigan locality in the central Bighorn Basin— YM-421: UM 64143 and 64178.

Description.— Two specimens are referred to this species. One is a fragment of the anterior part of a small dentary included as part of UM 64143. This has part of the crown of P_2 separated from roots of P_3 by a 4 mm diastema. The other is a partial dentary with crowns of $M_{2\text{-}3}$. These are distinctive in being small (M_2 measures 5.6 × 3.7 mm, M_3 measures 5.5 × 3.4 mm), in having the paraconid and metaconid closer together than either is to the protoconid, making a relatively closed trigonid, and in having relatively short, broad, and basined talonids. There is little question that this specimen belongs in *Prototomus*, and it is clearly significantly smaller than specimens referred to *P. secundarius*.

Discussion.— This, the type species of *Prototomus*, is clearly the least well known. The holotype is lost. No additional specimens from the San Juan Basin have ever been described.

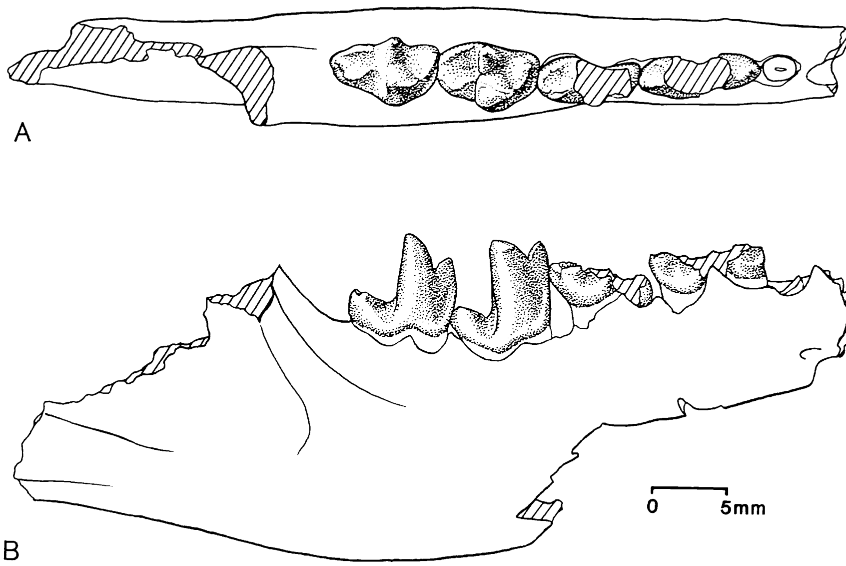

FIG. 17— Right dentary of *Prototomus secundarius*, UM 75570 from GR-16, with P_4-M_3. A, occlusal, and B, lateral view.

Matthew (1915) reported that no specimens of it were found in the Bighorn Basin. Dentaries from the Green River Basin questionably included here by Gazin (1962, p. 54) were referred to a new species of the carnivorous condylarth *Wyolestes* when restudied (Gingerich, 1982).

Prototomus secundarius Cope, 1875

Fig. 17

Prototomus secundarius Cope, 1875, p. 9.
Prototomus multicuspis Cope, 1875, p. 10.
Stypolophus secundarius, Cope, 1877, p. 115.
Stypolophus multicuspis, Cope, 1877, p. 116, Pl. 39:12-14.
Sinopa multicuspis, Matthew, 1901, p. 27; 1915, p. 80.
Sinopa secundaria, Matthew, 1915, p. 82, fig. 77.

Holotype.— USNM 1025, left dentary fragment with the talonid of P_4 and right dentary fragment with the talonid of M_2.

Type locality.— San Jose Formation of San Juan Basin, New Mexico.

Age and distribution.— *P. secundarius* is known from the late Graybullian, Lysitean, and possibly Lostcabinian subages of the Wasatchian land-mammal age. It is known with certainty from the San Juan Basin and the Bighorn Basin, but probably occurs in intervening basins as well.

Diagnosis.— Intermediate in size between *P. viverrinus* and *P. robustus.* Differs from earlier species of the genus in having talonids on lower molars a little shorter, broader, and more basined.

Included specimens.— Graybull River area localities in the central Bighorn Basin— GR-11: UM 75494 and 75525. GR-16: UM 75570. McCullough Peaks area localities— MP-6: UM 82454. MP-15: UM 86922. MP-43: UM 88310. MP-64: UM 91296. MP-75: UM 91470. MP-77: UM 91572. MP-87: UM 92009. MP-171: UM 94229. Yale-Michigan locality in the central Bighorn Basin— YM-45: UM 66010.

Description.— The type specimen of *Prototomus multicuspis*, USNM 1021 from the San Juan Basin, is a left maxilla with M^1 and a right maxilla with P^4-M^3, and this is still the best upper dentition known. P^4 has the distinct protocone typical of early Eocene hyaenodontids. The prominent labial cusp (metacone?) has a distinctly notched postmetacrista. M^1 and M^2 both have connate paracones and metacones, with distinctly notched postmetacristae. M^2 differs from M^1 in being a little larger and in having a more prominent parastyle. M^3 is broken, but it was clearly reduced in length, with little or no metacone and no postmetacrista.

The holotype dentary, USNM 1025 from the San Juan Basin, is important in establishing the size of *Prototomus* to which the specific name *secundarius* belongs. M_2 measures approximately 7.5 mm in length and 3.3 mm in width. It is also important in showing that *P. secundarius* had a shorter, broader, and more basined talonid on lower molars than is characteristic of earlier species of *Prototomus*.

USNM 1020 from the San Juan Basin is one of the best dentaries known to date. It shows P_3 and P_4 to have been long and narrow teeth with single apical cusps and smaller posterior talonid cusps. M_{1-3} have the paraconid and metaconid relatively close together, giving all three teeth a "closed" trigonid. The talonids on M_{2-3} are short, broad, and basined like the type specimen. The talonid on M_3 is narrower and a little longer than that on M_2.

The most complete dentary in our new collections from the Bighorn Basin is UM 75570 (Fig. 17), which adds little to knowledge of this species. Three specimens preserving alveoli for P_1 are consistent in showing this tooth to have been single-rooted. UM 75525 and 91572 preserve sizable diastemata between P_2 and P_3 and between P_1 and P_2, respectively.

A statistical summary of dental measurements is given in Table 13. Coefficients of variation of the lengths and widths of most cheek teeth are within the 4-8 range observed in modern carnivore species (Gingerich and Winkler, 1979).

Discussion.— The name *secundarius* is here conserved rather than *multicuspis* because the type specimen of *secundarius* includes lower teeth that are more useful for comparison, because *secundarius* is more informative as a name (accurately describing the size rank of this species), and because *multicuspis* has been widely and often incorrectly used for any early Eocene hyaenodontid of medium size. Cope's best specimen from a comparative point of view is not a type at all: it is USNM 1020, a left dentary with P_3-M_3 illustrated in Cope's Report upon the Extinct Vertebrata obtained in New Mexico (1877, Pl. 39:12), where it was referred to *Prototomus* (or *Stypolophus*) *multicuspis*. If correctly referred to *P. multicuspis* (and this probably was correct), it shows as no other known specimen could that *P. multicuspis* and *P. secundarius* are synonyms.

One specimen mentioned by Matthew (1915, p. 83) as being about the same size as *Prototomus secundarius*, AMNH 16120, a left dentary with M_{1-2}, was recently recognized as a good representative (and possibly a topotype) of *Wyolestes apheles* Gingerich (1981).

Prototomus robustus (Matthew, 1915)

Fig. 18

Stypolophus whitiae (in part), Osborn and Wortman, 1892, p. 110.
Prolimnocyon robustus Matthew, 1915, p. 70, fig. 62. Denison, 1938, p. 178.
Sinopa multicuspis (in part), Matthew, 1915, p. 80, figs. 72-73.
Paeneprolimnocyon mordax (in part), Van Valen, 1969, p. 116.
?*Paeneprolimnocyon mordax* (in part), Delson, 1971, p. 330, figs. 10-11 (pt.).

Holotype.— AMNH 15168, a fragmentary right dentary with the talonid of M_2 and the intact crown of M_3.

Type locality.— Specimen is said to come from "lower forks of Dorsey Creek" (AMNH specimen file), but it lacks a field number and this locality record has to be considered vague, even questionable, by comparison with other specimens that have precise locality information recorded in the field.

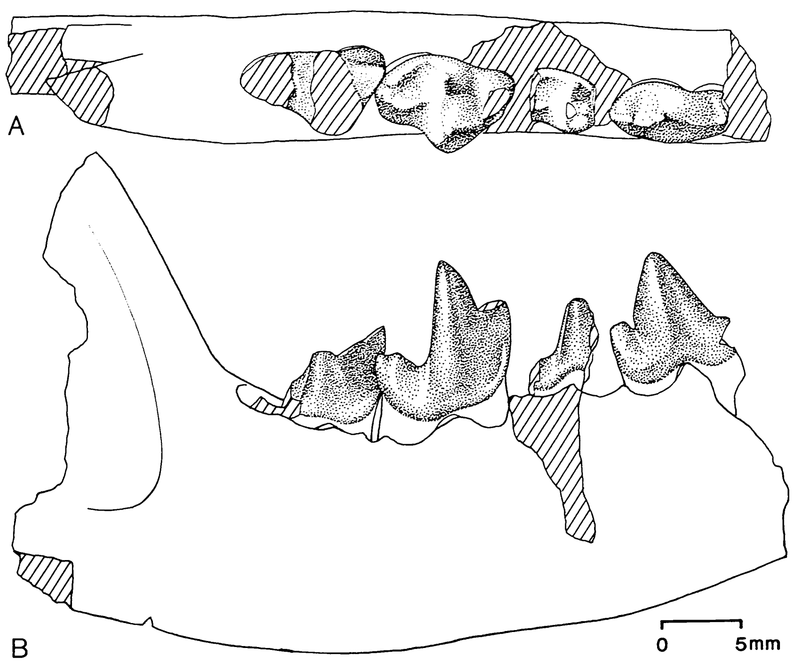

FIG. 18— Right dentary of *Prototomus robustus*, UM 73489 from SC-265, with P_4-M_3. A, occlusal, and B, lateral view.

Age and distribution.— *Prototomus robustus* is known from the middle and late Graybullian subages of the Wasatchian land-mammal age. It is presently known only from the Bighorn and Clarks Fork basins, Wyoming.

Diagnosis.— Largest species of *Prototomus*. Differs from its putative ancestor *P. martis* in averaging one to two normalized standard deviations larger. The type and at least one referred specimen of *P. robustus* also differ in exhibiting significant M_3 reduction.

Included specimens.— McCullough Peaks area localities— MP-17: UM 87010. MP-80: UM 91602. MP-96: UM 92160. MP-103: UM 92211. MP-113: UM 92324. MP-142: UM 93361. MP-163: UM 94009. MP-163: UM 94010. MP-171: UM 94223. Sand Coulee area localities— SC-111: UM 79896. SC-254: UM 73059. SC-256: UM 73553. SC-265: UM 73489. SC-303: UM 75722. SC-353: UM 88065. Yale-Michigan localities in the central Bighorn Basin— YM-320: UM 64236. YM-421: UM 64070, 64141, 64146, 64288, and 64500 (in part). YM-429: UM 92671 (in part). USNM 19468 from five miles south of Otto in the central Bighorn Basin is also included here.

Description.— Most specimens of this species are fragmentary, serving only to establish the presence of a large *Prototomus* where they are represented. UM 91602 includes a well preserved M^2, which resembles that in other species in having a connate paracone-metacone, a well separated protocone, a distinct paraconule and a smaller metaconule, a well developed parastyle, and a distinctly notched postmetacrista.

There is only one specimen that shows the number of P_1 roots: UM 93361 has a single-rooted P_1 like that of all other *Prototomus*. This specimen has the anterior premolars spaced more closely together than is typical of *Prototomus*. Otherwise, lower cheek teeth resemble those of *P. martis* very closely (Fig. 18).

A statistical summary of dental measurements is given in Table 14. Coefficients of variation of the lengths and widths of most cheek teeth are within the 4-8 range observed in modern carnivore species (Gingerich and Winkler, 1979).

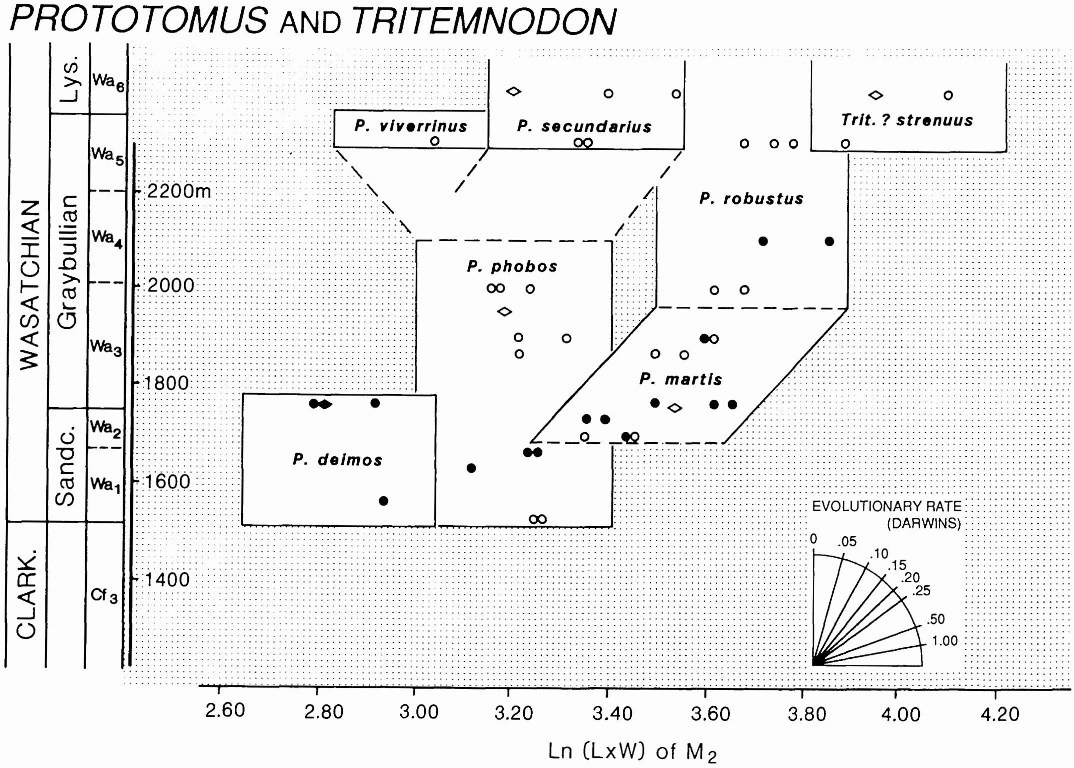

FIG. 19— Size-time plot showing stratigraphic distribution of species of *Prototomus* and *Tritemnodon*. Abscissa is size of M_2 as an indicator of overall body size. Ordinate is meter level in Clarks Fork Basin stratigraphic section. Solid figures represent specimens from known stratigraphic levels in the Clarks Fork Basin. Open figures represent specimens for which stratigraphic level must be inferred by faunal comparison. Diamonds show positions of type specimens. Dashed lines show approximate limits of mean ± two standard deviations in tooth size, fit to observed distributions of points. *Prototomus* made its first appearance at the beginning of the Wasatchian land-mammal age. *Tritemnodon?* made its first appearance in the late Graybullian subage. Late Graybullian (Wa_5) and Lysitean (Wa_6) specimens plotted here are all from the northern and central Bighorn Basin.

UM 64500 includes a virtually complete right humerus similar in size and form to that of *Arfia shoshoniensis*. It measures 91.2 mm in length, and 6.9 by ca. 11.8 mm in midshaft diameter. The proximal end, including the head, measures 20.2 mm in anteroposterior diameter, and 19.5 mm transversely across the greater and lesser tuberosities. The distal end measures 26.3 mm transversely. The condylar surface is cylindrical, measuring 7.3 mm in diameter. The humeral head is a little more tapered than that of *Arfia*, but it is similarly positioned well back relative to the shaft. The shaft is less strongly curved (sigmoid) in the sagittal plane than that of *Arfia*. The length of the deltopectoral crest cannot be determined due to breakage. There is a distinct supratrochlear vacuity, but it is much smaller than that of *Arfia*. UM 92671 includes the distal end of a right tibia and most of an articulating right astragalus. The astragalus is similar to that of *Arfia shoshoniensis* in general plan, but differs in being flatter, having a less developed medial shelf connecting the head to the body, and in having a much smaller astragalar foramen. It does have the posteromedial spiral facet for hind foot reversal found in *Arfia* and in other *Prototomus*.

Discussion.— The type specimen of *Prototomus robustus* is so fragmentary that it has long been problematical. The specimen was originally identified as *Prolimnocyon* by Matthew (1915) because of its reduced M_3, but this is less reduced than that of any other *Prolimnocyon*. No new or more complete specimens of such a large *Prolimnocyon* have ever been found in the type area, the central Bighorn Basin, in spite of many decades of intensive collecting since the type was found in 1910. None have been found with such a large M_3 either. This raises the question of whether Matthew was correct in referring *P. robustus* to *Prolimnocyon*. The right dentary of AMNH 97, a specimen collected in the Bighorn Basin in 1891, is the only dentary similar in size, preservation, and age to the type that also has a similarly reduced M_3. Osborn and Wortman (1892) identified AMNH 97 as *Stypolophus whitiae*, but it has never been further described or discussed. While M_3 is reduced on the right side, AMNH 97 also includes an associated left dentary with little or no reduction in the size of M_3 relative to preceding teeth. The left dentary of AMNH 97 is similar in turn to other large specimens here referred to *Prototomus*. M_3 reduction is here interpreted as a variable characteristic within some individuals and within the species. There is no other specific name available for large *Prototomus*, and *robustus* is here employed as a name for the largest species of *Prototomus* from middle and late Graybullian strata (recognizing of course that discovery of such a large *Prolimnocyon* in the Bighorn Basin could render this conservative decision moot).

The size distribution of specimens referred to all Bighorn and Clarks Fork basin species of *Prototomus* is shown in Figure 19.

Prototomus? vulpeculus (Matthew, 1915)

Fig. 20A,B

Sinopa vulpecula Matthew, 1915, p. 80, fig. 75-76.
Sinopa cf. *S. vulpecula*, Gazin, 1962, p. 55, Pl. 6:1-2.

Holotype.— AMNH 15606, right dentary with C_1 and P_2-M_3.

Type locality.— Five miles north of Parker Spring in the central Bighorn Basin.

Age and distribution.— Lostcabinian subage of Wasatchian land-mammal age, early Eocene. This species is known from the Bighorn and Green River basins, Wyoming.

Diagnosis.— Intermediate in size between *P. secundarius* and *P. robustus*. Questionably different from the former, and clearly different from the latter in having large diastemata preceding and following P_1. Differs from all other species of *Prototomus* in having less symmetrical upper molars, with a more reduced parastyle, particularly on M^2.

Included specimens.— No new specimens of this species are available.

Discussion.— Figure 20 shows how upper molars of *P.? vulpeculus* differ from those of typical *Prototomus* in being more skewed and less symmetrical, with the parastyle greatly reduced on M^2. All of the described dentaries are distinctive in being greatly elongated anteriorly, with substantial diastemata between C_1 and P_1, between P_1 and P_2, and sometimes between P_2 and P_3. This species may represent a new genus.

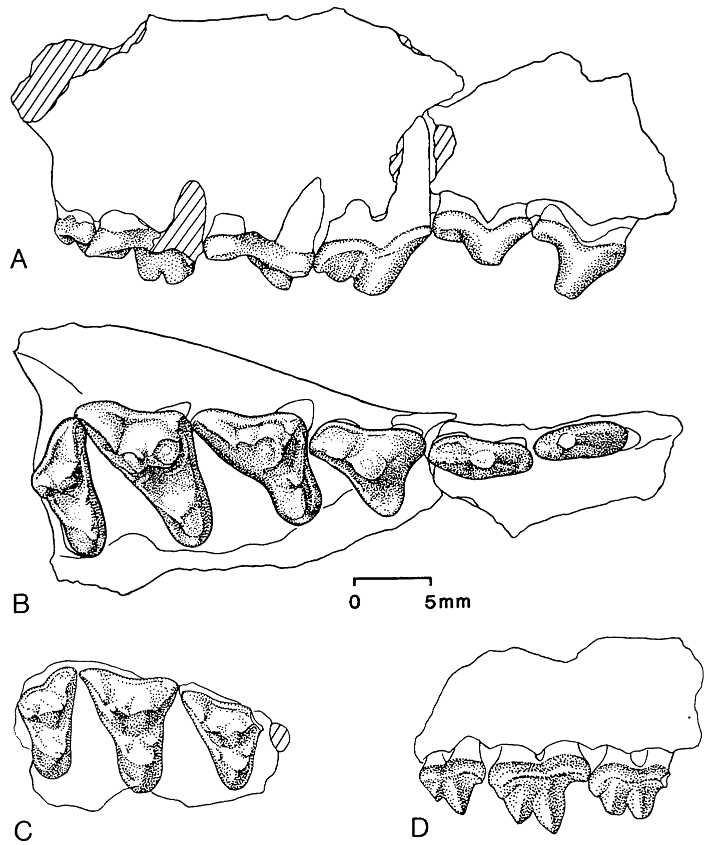

FIG. 20— Right maxilla of *Prototomus? vulpeculus* with P^2-M^3, USNM 19347 of Lostcabinian age from La Barge, compared to right maxilla of *Prototomus phobos* with M^{1-3}, UM 74134 (reversed) of early Graybullian age from SC-64. Note greater skewing of upper molars in *P.? vulpeculus*.

Tritemnodon Matthew, 1906

Limnocyon (in part), Marsh, 1872, p. 204.
Prototomus (in part), Cope, 1875, p. 9; 1884, p. 290.
Stypolophus (in part), Cope, 1877, p. 109; 1884, p. 285.
Sinopa (in part), Matthew, 1901, p. 23; 1915, p. 71. Wortman, 1902, p. 124.
Tritemnodon Matthew, 1906, p. 205.; 1909, p. 474; 1915, p. 84.

Type species.— *Limnocyon agilis* Marsh, 1872.

Included species.— *Tritemnodon agilis* (Marsh, 1872), and questionably *T. strenuus* (Cope, 1875).

Age and distribution.— Middle Wasatchian(?) through Bridgerian land-mammal ages, early and middle Eocene, of western North America.

Diagnosis.— *Tritemnodon* differs from contemporary middle Eocene *Sinopa* in having a connate paracone-metacone like that of *Prototomus.* It differs from early Eocene *Prototomus* in having a reduced metaconid, giving it a more open trigonid, especially on M_3.

Discussion.— The type species of *Tritemnodon*, *T. agilis* (Marsh, 1872), comes from sediments of the Bridgerian land-mammal age, middle Eocene, and the genus is known with certainty only

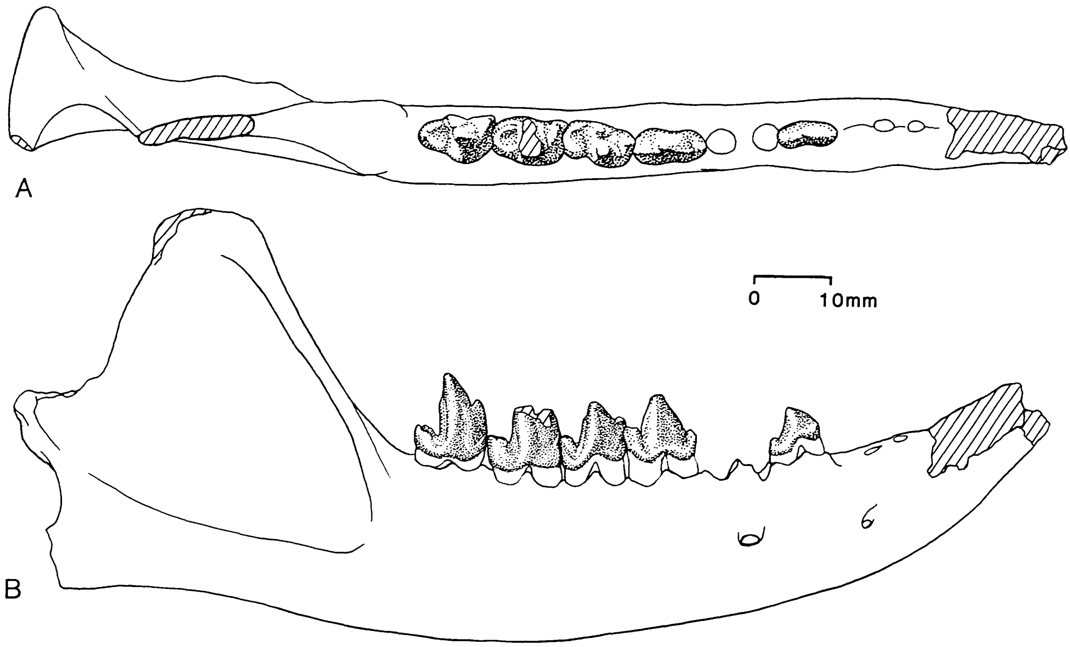

FIG. 21— Right dentary of *Tritemnodon? strenuus*, UM 21186, with alveoli for double-rooted P_1, P_2, and P_4-M_3. A, occlusal, and B, lateral view. Specimen is from northwest of Regina, on the east side of the road to Lindrith, in the San Juan Basin of New Mexico (collected in 1939).

from the middle Eocene. *T. strenuus* is referred questionably to *Tritemnodon*, and hence downward extension of the stratigraphic range of *Tritemnodon* must be considered questionable as well.

Tritemnodon? strenuus (Cope, 1875)

Fig. 21

Prototomus strenuus Cope, 1875, p. 10.
Stypolophus strenuus, Cope, 1877, p. 117, Pl. 39: 11.
Stypolophus hians Cope, 1877, p. 118, Pl. 38: 12-30.
?*Stypolophus strenuus*, Cope, 1881, p. 192.
?*Stypolophus whitiae* Cope, 1882, p. 161; 1884, p. 292, Pl. 25b: 8-14.
Sinopa strenua, Matthew, 1901, p. 26; 1915, p. 74, figs. 66-67.
Sinopa hians, Matthew, 1901, p. 25; 1915, p. 75, figs. 68-71.
Tritemnodon strenuus, Van Valen, 1965, p. 639. Guthrie, 1967, p. 15.
Tritemnodon hians, Van Valen, 1965, p. 639.
?*Tritemnodon whitiae*, Matthew, 1906, p. 207, figs. 1f, 2g; 1915, p. 84. Van Valen, 1965, p. 639.

Holotype.— USNM 1023, upper canine and left and right dentaries with P_4-M_3, somewhat deformed, broken, and incompletely prepared.

Type locality.— San Jose Formation of the San Juan Basin, New Mexico.

Age and distribution.— *Tritemnodon? strenuus* is known from the late Graybullian, Lysitean, and Lostcabinian subages of the Wasatchian land-mammal age, early Eocene, and it is known from the Bighorn, Clarks Fork, Green River, and Wind River basins of Wyoming and the San Juan Basin of New Mexico.

Diagnosis.— Largest early Eocene hyaenodontid with a confluent paracone and metacone. Further differs from species of *Prototomus* in having a double-rooted P_1, and in showing a tendency toward metaconid reduction, with a more open trigonid on lower molars.

Included specimens.— Graybull River area locality in the central Bighorn Basin— GR-11: UM 75483. McCullough Peaks area localities— MP-81: UM 91633. MP-82: UM 92687. MP-119: UM 92393. MP-151: UM 93709. MP-159: UM 93980. UM 21186 from northwest of Regina in the San Juan Basin, New Mexico, is also included here.

Description.— Specimens of this species are well described and illustrated by Matthew (1915: figs. 66-71). Matthew's specimens, like the new specimens included here, consistently exhibit a double-rooted P_1, and some show a tendency toward reduction of the metaconid on lower molars, particularly M_3. UM 21186 (Fig. 21) is particularly interesting in exhibiting both of these characteristics and in coming from the type area in the San Jose Formation of the San Juan Basin.

A statistical summary of dental measurements is given in Table 15. Coefficients of variation of the lengths and widths of most cheek teeth are within the 4-8 range observed in modern carnivore species (Gingerich and Winkler, 1979).

Discussion.— Inclusion of *T. strenuus* in the genus *Tritemnodon* must be considered questionable as it is intermediate in some characteristics (e.g., metaconid reduction) between typical early Eocene *Prototomus* and middle Eocene *Tritemnodon*, and it is distinctively specialized in others (e.g., double-rooted P_1).

Pyrocyon, new genus

Type species.— Pyrocyon dioctetus, new species.

Included species.— Type species only.

Age and distribution.— Middle Wasatchian land-mammal age, early Eocene, of western North America.

Diagnosis.— Differs from other hyaenodontids in having crowded premolars, lightly crenulated enamel, P_1 double-rooted, P_3 lower-crowned than P_2, and lower molars with anteriorly placed paraconids and reduced metaconids, making the trigonids more open than in *Prototomus*. These differences are summarized in the key in Figure 27.

Etymology.— Pyr, Gr., fire, and *kyōn* (masc.), dog, in memory of the fires burning Yellowstone Park and filling the northern Bighorn Basin with smoke in the summer of 1988 when this species was discovered.

Discussion.— Five genera and seven species, representing seven distinct evolutionary lineages, are known from the early Wasatchian land-mammal age. Discovery of *Pyrocyon* brings to four the number of genera and six the number of distinct evolutionary lineages known from the late Graybullian subage of the middle Wasatchian.

Pyrocyon dioctetus, new species

Fig. 22

Holotype.— UM 94757, both upper canines, left maxillary fragment with M^2, left dentary with C_1-M_3, right dentary with P_1 and P_4-M_3, and numerous postcranial elements including a complete right humerus, collected by PDG.

Type locality.— University of Michigan locality MP-193 in the northern Bighorn Basin: SW$\frac{1}{4}$, NE$\frac{1}{4}$, Section 31, T54N, R99W, Park County, Wyoming.

Age and distribution.— Pyrocyon dioctetus is known only from the late Graybullian subage of the Wasatchian land-mammal age, early Eocene, and it is presently known only from the type locality in the northern Bighorn Basin.

Diagnosis.— As for the genus.

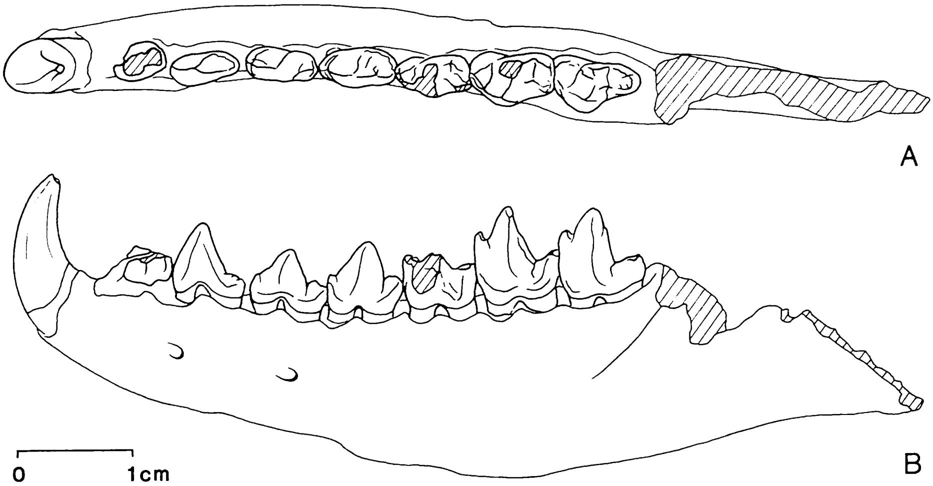

FIG. 22— Left dentary of *Pyrocyon dioctetus*, UM 94757 (holotype) from MP-193, with C_1, double-rooted P_1, and P_2-M_3. A, occlusal, and B, lateral view.

Etymology.— *di*, Gr., double, *octo*, eight, and *etos*, year.

Included specimens.— Holotype only.

Description.— The upper canines have thick straight roots and smaller slightly curved crowns. The canine crowns appear more robust than those of other early Eocene hyaenodontids. The only upper molar is a left M^2 in a piece of maxilla. This has the confluent or connate paracone-metacone typical of generalized hyaenodontids, a well separated protocone flanked by a small paraconule and smaller metaconule, a moderately large parastyle and a distinctly notched postmetacrista connecting the metacone and metastyle.

The lower canine is robust, with a distinctly curved crown. P_1, preserved in place in the right dentary, has a single apical cusp near the front of the crown with a curved crest sloping downward posteriorly. It is distinctly double-rooted. P_2 is a much larger tooth with a high and bluntly pointed apical cusp. There is a distinct posterior accessory cuspule at the base of the crown. P_3 and P_4 are similar in shape to P_2, but each has an anterior basal cusp not seen in P_2. Both have bluntly pointed crowns, and the crown of P_3 is conspicuously lower than that of either P_2 or P_4. The premolars are all crowded together in the dentary with little or no space between them.

All three lower molars have a slightly more open trigonid than is typical of *Prototomus*, with the paraconid positioned more anteriorly relative to the other trigonid cusps and the metaconid reduced somewhat in size. The talonids on M_1 and M_2 are rather short, broad, and shallowly basined, while that on M_3 is narrower but still distinctly basined. Mental foramina are positioned beneath the anterior root of P_2 and the posterior root of P_3.

Measurements of the dentition of the holotype are listed in Table 16.

Postcranial elements associated with the holotype include a number of vertebral centra and parts of both fore and hind limbs. Dentally *Pyrocyon dioctetus* is similar in size to *Prototomus martis*, and it is natural to compare their postcranials. Most of the glenoids of both scapulae are preserved. These are similar in maximum diameter to the glenoid of *P. martis* (Fig. 15A), but more constricted in minimum diameter. The right humerus is nearly complete, and much of the left is preserved as well. The humerus of *Pyrocyon* is very similar in size to that of *P. martis* (Fig. 15B,C) but it is a little shorter, measuring only ca. 74 mm in length. The difference is all in the upper part of the shaft, meaning that the deltopectoral crest does not extend as far relative to the length of the bone (it stops at about mid-length). Unlike both *Arfia* and *Prototomus*, there is no supratrochlear vacuity. The proximal end of the right ulna is preserved, but poorly, and little can be said about it. Proximal and distal ends of both radii are preserved. These are similar to proximal and distal radii of *Prototomus* illustrated here (Fig. 15F,G).

Parts of both femora and tibiae are preserved, but little can be said about these. There is a large medial malleolus on the right distal tibia, and it has the same sloping astragalar articulation seen in *Arfia*. The body of the left astragalus is a little larger than that illustrated for *P. martis* (Fig. 15H) but otherwise very similar. The trochlea is shallowly grooved, and a spiral facet is present on the posteromedial surface facilitating hind foot reversal like that described above for *Arfia* and *Prototomus.*

Discussion.— The type locality of *Pyrocyon dioctetus* is high in the McCullough Peaks, in an area difficult to reach on foot. Cranial and postcranial remains collected in 1988 have a number of fresh breaks, and hopefully connecting fragments will be found when the site is revisited in the future. This should make possible a more detailed comparison of postcranial anatomy with the better known *Prototomus.*

Galecyon, new genus

Sinopa (in part), Matthew, 1915, p. 73.
Prototomus (in part), Van Valen, 1965, p. 639.
Paeneprolimnocyon (in part), Van Valen, 1969, p. 116.
?Paeneprolimnocyon, Delson, 1971, p. 330.
Sinopa (in part), MacIntyre and Guthrie, 1979, p. 1036.

Type species.— *Sinopa mordax* Matthew, 1915.

Included species.— Type species only.

Age and distribution.— Early Wasatchian land-mammal age, early Eocene, of western North America.

Etymology.— *Gale*, Gr., polecat, and *kyōn* (masc.), dog. Most specimens of this genus come from the Sand Coulee area west of Polecat Bench in Wyoming.

Diagnosis.— Differs from other hyaenodontids in combining robust canines, a short deep dentary, single-rooted P_1, short and broadly basined talonids on M_{1-2}, and reduced M_3. These differences are summarized in the key in Figure 27.

Discussion.— Matthew (1915) recognized the distinctiveness of the one specimen he had available, making it the type of a new species of the broadly conceived genus *Sinopa.* Van Valen (1965) first transferred this to *Prototomus*, and then (1969) to *Paeneprolimnocyon.* Van Valen (1969) also synonymized middle to late Wasatchian *Prolimnocyon robustus* (here *Prototomus robustus*) with early to middle Wasatchian *Paeneprolimnocyon mordax.* Delson (1971) described a second specimen from the early Wasatchian of the Powder River Basin, and noted that the major question concerning *mordax* was whether it should be referred to *Prototomus*, to *Prolimnocyon*, or to *Paeneprolimnocyon.* Six new specimens are now available, all from the early to middle Wasatchian of the Clarks Fork Basin. These, together with the type and Delson's specimen, are consistent in having distinctively short blocky lower molars and other differences precluding reference to any previously known genera.

Galecyon mordax (Matthew, 1915)

Fig. 23

Sinopa mordax Matthew, 1915, p. 73, fig. 64. MacIntyre and Guthrie, 1979, p. 1036.
?Paeneprolimnocyon mordax, Delson, 1971, p. 330, figs. 10-11 (pt.).

Holotype.— AMNH 16157, left and right lower jaws.

Type locality.— Clarks Fork Basin, Wyoming.

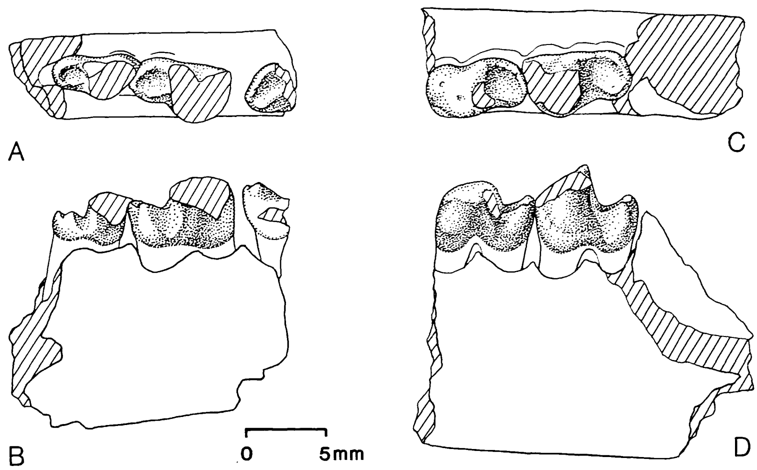

FIG. 23— Right dentary of *Galecyon mordax*, UM 76227 from SC-41, with talonid of M_1 and $M_{2\text{-}3}$. A, occlusal, and B, lateral view. Left dentary of *Galecyon mordax*, UM 69794 from SC-213, with $M_{1\text{-}2}$. C, occlusal, and D, lateral view.

Age and distribution.— *Galecyon mordax* is known from the middle and late Sandcouleean and early Graybullian subages of the early and middle Wasatchian land-mammal age, early Eocene. It is known only from the Clarks Fork and Powder River basins, Wyoming.

Diagnosis.— As for the genus.

Included specimens.— Sand Coulee area localities— SC-2: UM 85887. SC-15: UM 75317. SC-41: UM 76227. SC-161: UM 68805. SC-213: UM 69794. SC-317: UM 77337.

Description.— The type specimen is still the most informative specimen. A left dentary, UM 85887 from locality SC-2, possibly the type locality, is nearly as complete. It preserves the heavy symphysis and robust lower canine with a massive root seen in the holotype. AMNH 16157 is still the only specimen to preserve the single-rooted alveolus for P_1 and to show the close spacing of anterior premolars. Crowns of $P_{2\text{-}4}$ are distinctive in having large trenchant posterior cusps. P_4 in UM 85887 has a strong anterior cusp and two posterior cusps flanking its apical cusp, while UM 68805 has a smaller anterior cusp and a single posterior cusp. M_1 and M_2 have relatively short, broad, blocky crowns, with a broad basined talonid (Fig. 23). Crowns of M_3 are preserved in UM 75317 and 76227. The former is moderately reduced like that in the holotype, while the latter is small and narrow like that in AMNH 56320 described by Delson (1971).

A statistical summary of dental measurements is given in Table 17.

Discussion.— *Galecyon mordax* is still poorly known. Nothing is known of the upper dentition or the postcranial skeleton. However the material at hand is sufficient to support Matthew's recognition of a distinct species for this form and, further, to separate it from *Prototomus*, *Prolimnocyon*, and *Sinopa*, with which it has been compared previously. *Paeneprolimnocyon* is now regarded as a junior synonym of the miacid *Oodectes* and not a hyaenodontid at all (MacIntyre and Guthrie, 1979).

Subfamily LIMNOCYONINAE Wortman, 1902

Prolimnocyon Matthew, 1915

Prolimnocyon Matthew, 1915, p. 67.
Prototomus (in part), McKenna, 1960, p. 92.

Type species.— *Prolimnocyon atavus* Matthew, 1915.

Included species.— *Prolimnocyon haematus*, new species; *P. atavus* Matthew, 1915; *P. antiquus* Matthew, 1915. *P. elizabethae* Gazin, 1952, is questionably distinct from *P. atavus* or *P. antiquus*.

Age and distribution.— Wasatchian land-mammal age, early Eocene, of western North America.

Diagnosis.— Differs from other hyaenodontids in showing reduction of M^2 and extreme reduction of M^3 and M_3. Other differences are summarized in the key in Figure 27.

Discussion.— *Prolimnocyon* is a distinctive hyaenodontid genus easily recognized by its extreme reduction of M^3 and M_3. Isolated M_1 and M_2 resemble *Prototomus* but can be distinguished, given adequate comparative specimens, by their longer, narrower crowns, and talonids more angled labially relative to the trigonid.

McKenna's (1960) subjugation of *Prolimnocyon* as a synonym of *Prototomus*, discussed in an opening section of this paper, reflected a legitimate technical question he raised about the holotype of the type species of *Prototomus*, *P. viverrinus*, rather than ambiguity in delimitation or recognition of *Prolimnocyon*. The holotype of *P. viverrinus* may, if ever relocated, turn out to represent *Prolimnocyon* rather than the group here labelled *Prototomus*, but evidence presently favoring this possibility is too weak to warrant the nomenclatural disruption such an outcome would require.

Prolimnocyon haematus, new species
Figs. 24, 25

Prolimnocyon atavus (in part), Matthew, 1915, p. 68. Delson, 1971, p. 332, fig. 12 (pt.). Bown, 1979, p. 90

Holotype.— UM 65622, cranium with left C^1-P^1 and P^4-M^2, right C^1-P^2 and $M^{1\text{-}2}$, and a right dentary with P_4-M_2, collected by Thomas Abdelnour.

Type locality.— University of Michigan locality SC-54 in the Clarks Fork Basin: NW$\frac{1}{4}$, SE$\frac{1}{4}$, Section 26, T56N, R102W, Park County, Wyoming.

Age and distribution.— *Prolimnocyon haematus* is known from the Sandcouleean and early Graybullian subages of the early and middle Wasatchian land-mammal age, early Eocene. It is known principally from the Clarks Fork Basin, but also from the southern Bighorn Basin and from the Powder River Basin, Wyoming.

Diagnosis.— Differs from *P. atavus* and *P. antiquus* in being about two normalized standard deviations smaller, in consistently having P_1 single-rooted, and in having a double-rooted M_3.

Etymology.— Greek *haimatos*, blood, in reference to the red oxidized iron matrix adhering to the holotype.

Included specimens.— Sand Coulee area localities— SC-2: UM 67501, 67511, 76358, 76366, 80039, and 87406. SC-12: UM 64806. SC-17: UM 64984. SC-54: UM 65622 and 68584. SC-87: UM 79833. SC-96: UM 77365. SC-133: UM 68482. SC-160: UM 68138. SC-161: UM 68637. SC-207: UM 69480 and 69499. SC-210: UM 72223. SC-213: UM 79575, 81848, 81854, and 84697. SC-300: UM 75121. SC-328: UM 80232. Yale-Michigan locality in the central Bighorn Basin— YM-397: UM 63885.

The following specimens described by Bown (1979) probably belong here: UW 9839 and 9938. These span the 46 to 64 meter interval in Bown's measured stratigraphic section.

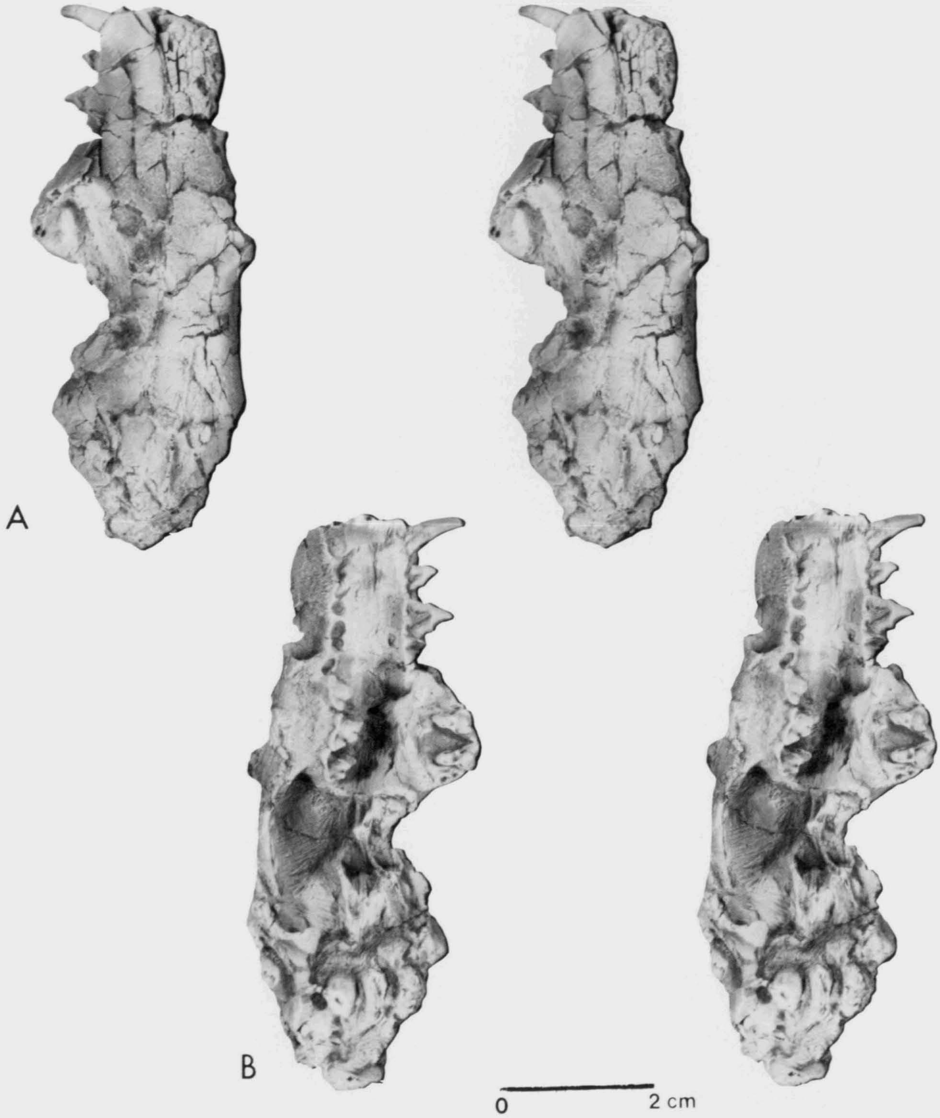

FIG. 24— Stereophotograph of cranium of *Prolimnocyon haematus*, UM 65622 (holotype) from SC-54. Cranium preserves left C^1, $P^{1\text{-}2}$, and $M^{1\text{-}2}$, and right C^1, P^1, and P^4-M^2. Small alveoli for double-rooted M^3 are visible behind M^2 on the left side. Natural size.

Description.— The cranium of the holotype is deformed, but unusually complete for a Clarks Fork Basin mammal (Fig. 24). It measures 75 mm in length as preserved, and this is probably close to the actual length in life. The width of the skull is more distorted and cannot be measured or even reliably estimated. The dorsal surface of the braincase is remarkably smooth for a car-

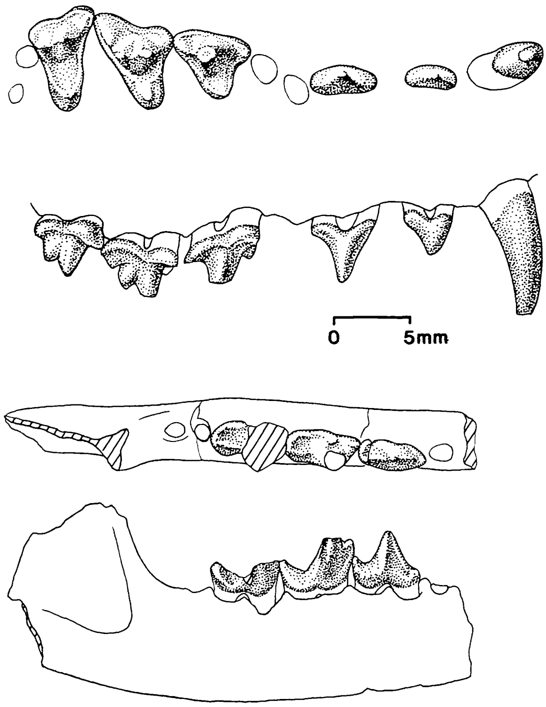

FIG. 25— Right maxilla and dentary of *Prolimnocyon haematus*, UM 65622 (holotype) from SC-54. Maxilla preserves C^1, double-rooted P^1, P^2 (reversed from left side), P^4-M^2, and alveoli for M^3 (reversed from left side). A, occlusal, and B, lateral view. Dentary preserves P_4-M_2 and alveoli for double-rooted M_3. C, occlusal, and D, lateral view.

nivorous mammal, with only the slightest trace of a sagittal crest, and little evidence of a nuchal crest. The basicranium is poorly preserved and nothing can be stated about the course of the carotid artery from this specimen.

The upper dentition of the holotype (Fig. 25A,B) includes all of the cheek teeth except P^3 and M^3. The upper canine is a gracile tooth with a moderately curved crown. P^1 is double-rooted, with a single narrow apical cusp and no accessory cuspules. P^2 is similar, but the apical cusp is higher and more pointed. The crown of P^3 is preserved in UM 80039. It is narrow, with only a very slight swelling in the position of the protocone. The posterior crest coming up the back of the apical cusp makes a sharp turn near the base of the crown. Enamel on the lingual side of the apical cusp is furrowed in a distinctive way. P^4 in the holotype and in UM 80039 has a lingual profile similar to that of P^3, but both have a distinct protocone (worn in UM 65622). P^4 in UM 80039 has the lingual furrowing of the enamel seen on P^3. M^1 has a confluent paracone and metacone, with the protocone set off lingually, little development of a parastyle, but exaggerated development of a metastyle. M^2 is similar, but with the metacone reduced in size, the parastyle well developed, and the metastyle very weak. The crown of M^3 is not preserved in any specimen, but alveoli in the holotype indicate it to have been very reduced in size but still double-rooted.

The holotype, UM 65622, includes a dentary with P_4 and M_{1-2} (Fig. 25C,D). The most complete anterior dentary is UM 64984. It has C_1 with most of a slender curved crown. P_1 is a small, forwardly inclined, single-rooted tooth with the apical cusp broken and a very small posterior basal cuspule. All three other specimens preserving alveoli for P_1 show this tooth to have been single-rooted as well. P_2 has a high apical cusp located near the front of the crown, with a small

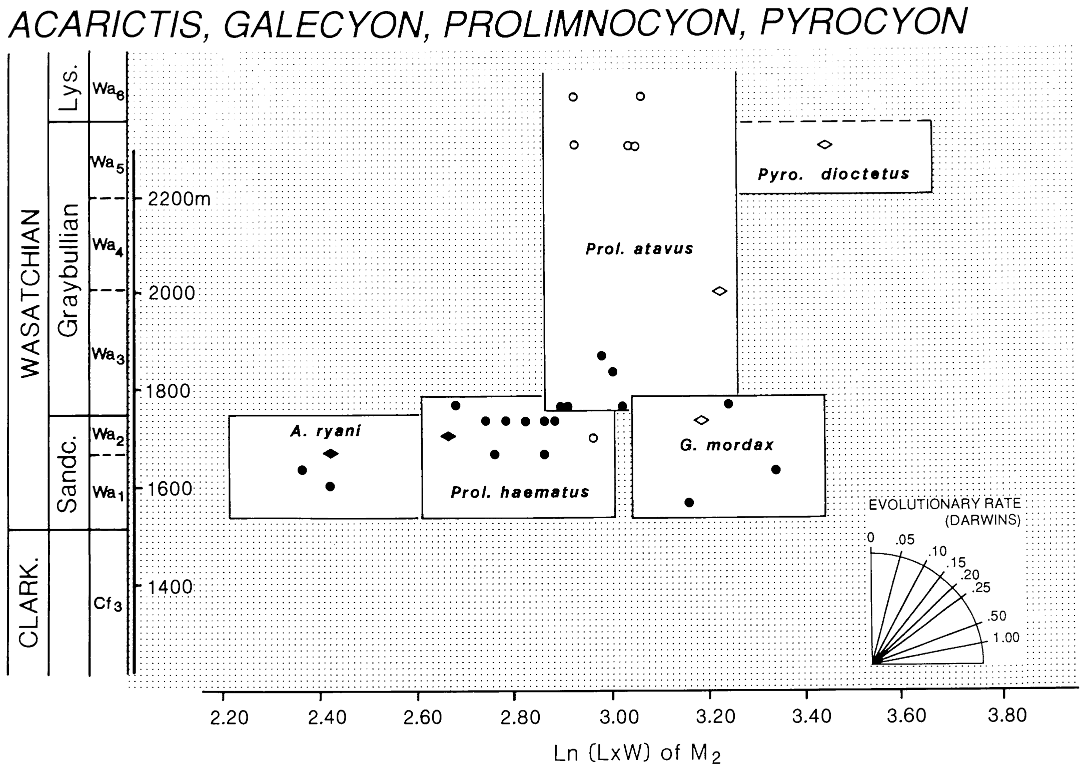

FIG. 26— Size-time plot showing stratigraphic distribution of species of *Acarictis*, *Galecyon*, *Prolimnocyon*, and *Pyrocyon*. Abscissa is size of M_2 as an indicator of overall body size. Ordinate is meter level in Clarks Fork Basin stratigraphic section. Solid figures represent specimens from known stratigraphic levels in the Clarks Fork Basin. Open figures represent specimens for which stratigraphic level must be inferred by faunal comparison. Diamonds show positions of type specimens. Dashed lines show approximate limits of mean ± two standard deviations in tooth size, fit to observed distributions of points. *Acarictis*, *Prolimnocyon*, and *Galecyon* made first appearances at or near the beginning of the Wasatchian land-mammal age. *Pyrocyon* made its first appearance in the late Graybullian subage. Late Graybullian (Wa_5) and Lysitean (Wa_6) specimens plotted here are all from the northern and central Bighorn Basin. Both *Prolimnocyon haematus* and *Prol. atavus* are present in samples from the same locality (SC-213) at the 1760 meter level in the Clarks Fork Basin.

posterior cuspule as well. P_3 is preserved in UM 80232. It has a more centrally located apical cusp, a small anterior cuspule, and a larger posterior cuspule. P_4 is similar, but with a more distinct anterior cusp and a larger posterior cusp. M_1 has a slightly longer and narrower crown than other hyaenodontids, with the paraconid and metaconid moderately well separated. The talonid is narrow but distinctly basined and it is usually more angled labially than is typical of other hyaenodontids. M_2 is similar, but a little shorter, and higher crowned. M_3 is greatly reduced in size by comparison to M_1 and M_2, and it has a relatively open trigonid and a short narrow talonid. Thirteen specimens preserve alveoli or roots showing that this tooth was consistently double-rooted. The premolars are closely spaced, and there are mental foramina beneath P_1 and beneath the anterior root of P_3.

Measurements of the holotype of *Prolimnocyon haematus* are given in Table 18, and a statistical summary of dental measurements for the species is given in Table 19. Coefficients of variation of the lengths and widths of most cheek teeth are within the 4-8 range observed in modern carnivore species (Gingerich and Winkler, 1979).

Discussion.— Matthew (1915, p. 68) first suggested that a Sandcouleean specimen in the AMNH Clarks Fork Basin collection was "smaller and perhaps a more primitive mutant." New and much larger collections from the Clarks Fork Basin substantiate the distinctiveness of this form.

Prolimnocyon atavus Matthew, 1915

Prolimnocyon atavus Matthew, 1915, p. 68, figs. 57 (pt.), 58-61. Denison, 1938, p. 178.
Prototomus viverrinus (in part), McKenna, 1960, p. 92, fig. 49.

Holotype.— AMNH 16816, lower jaw and fragments of skeleton.

Type locality.— Head of Ten Mile Creek in the Bighorn Basin, Wyoming

Age and distribution.— *Prolimnocyon atavus* is known from the Graybullian and Lysitean subages of the middle and late Wasatchian land-mammal age, early Eocene. It is known principally from the Bighorn and Clarks Fork basins in Wyoming, but also from the Sand Wash Basin of Colorado, and the San Juan Basin of New Mexico.

Diagnosis.— Differs from *P. haematus* in being about two normalized standard deviations larger, in having a double-rooted P_1, and in including at least one specimen with a single-rooted M_3. May differ from *P. antiquus* in including specimens with a double-rooted M_3.

Included specimens.— Foster Gulch area locality— FG-103: UM 87285. Graybull River area locality in the central Bighorn Basin— GR-16: UM 75555. McCullough Peaks area localities— MP-41: UM 88275. MP-43: UM 88309. MP-45: UM 86799. MP-162: UM 94006. MP-167: UM 94084. Sand Coulee area localities— SC-145: UM 67292. SC-192: UM 85717 and 85737. SC-213: UM 71086, 71130, and 81842. SC-225: UM 78960. SC-303: UM 75732. Yale-Michigan localities in the central Bighorn Basin— YM-45: UM 66010 and 66010. YM-143: UM 61763. YM-421: UM 64182. YM-425: UM 64296. YM-433: UM 72635.

Description.— Available specimens add little to Matthew's (1915) description of this species. UM 75555, like several of Matthew's specimens, preserves roots for a double-rooted P_1. UM 64182 clearly has only a single alveolus for M_3.

A statistical summary of dental measurements is given in Table 20.

Discussion.— *Prolimnocyon haematus* and *P. atavus* are both found at the 1760 meter level in the Clarks Fork Basin stratigraphic section, and both species are found together at locality SC-213. Coexistence indicates that these two species are not simply stages of a single evolving lineage, but represent two distinct lineages.

There is considerable variation in tooth size and in alveolus number within the specimens here grouped as *P. atavus*, and these may well be separable as distinct lineages when enough specimens are available. It is reasonable to expect that two forms may have coexisted through much of late Graybullian, Lysitean, and even Lostcabinian time. Matthew (1915) described one Lostcabinian species, *P. antiquus*, and Gazin (1952) described another, *P. elizabethae*. Neither, either, or both may be valid, but new specimens will be required before this problem can be solved.

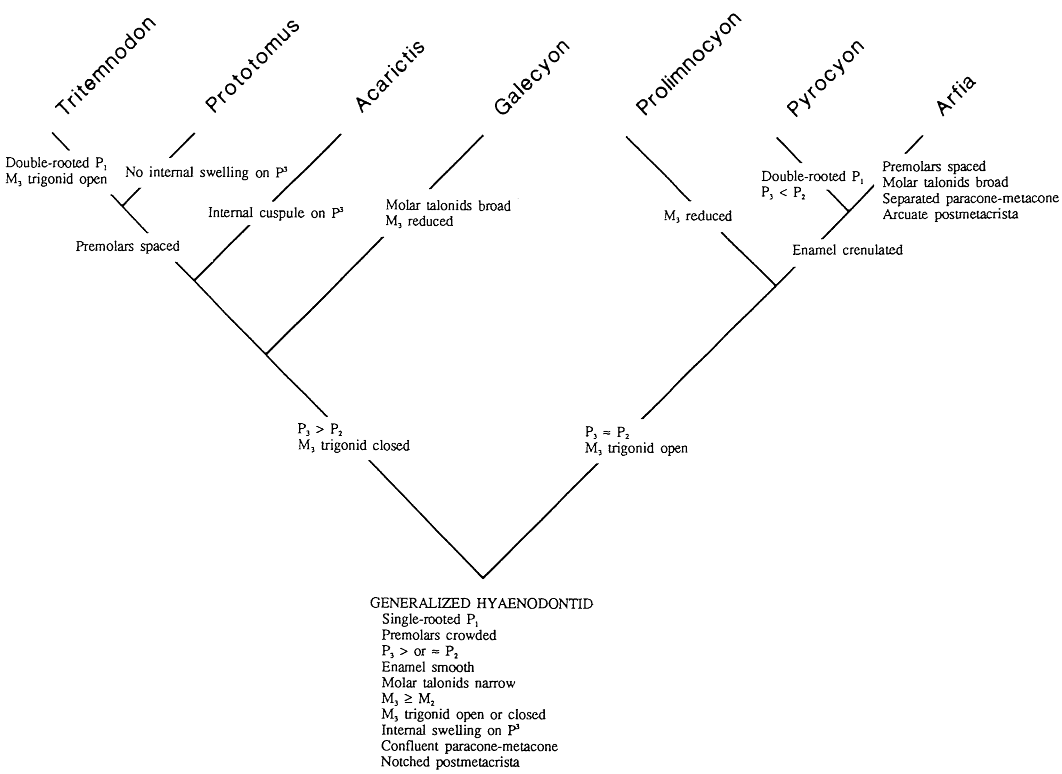

FIG. 27— Cladogram key to the North American early Eocene genera of Hyaenodontidae. Principal characteristics distinguishing genera of North American early Eocene hyaenodontids are indicated at appropriate nodes. Key shown here is one of nine equally most-parsimonious cladograms (length = 17, consistency index = 0.824) derived from exhaustive search of all trees using PAUP (Swofford, 1985; with characters unordered and unweighted, midpoint rooting).

SYSTEMATICS AND MORPHOMETRICS

Measurement has value beyond simple description. Carnivorous mammals, like the hyaenodontid creodonts studied here, are often diverse in form. They vary subtly within a standard plan, and this requires comparison in terms of shape as well as size. Ideally, all measurements are analyzed simultaneously, but this is rarely feasible in paleontological studies where most measurements are usually missing for most specimens. It is usually necessary to concentrate on informative and well represented subsets of measurements. In hyaenodontids, the third lower molar is one such subset. M_3 is the tooth most often preserved unworn, and it is the tooth that shows the greatest range of variation in both size and shape.

Five measurements were made on M_3 whenever possible: crown length, L; crown width, W; trigonid length, TRL; trigonid width, TRW; and trigonid height, TRH. All five measurements were available for only 39 specimens in this study. Trigonid height is the most limiting measurement because trigonid cusps are often subject to both wear and breakage. Removal of TRH increased the sample of M_3s with the remaining four measurements to 62. These were log-proportioned (log-transformed), and studied using principal components analysis of covariance.

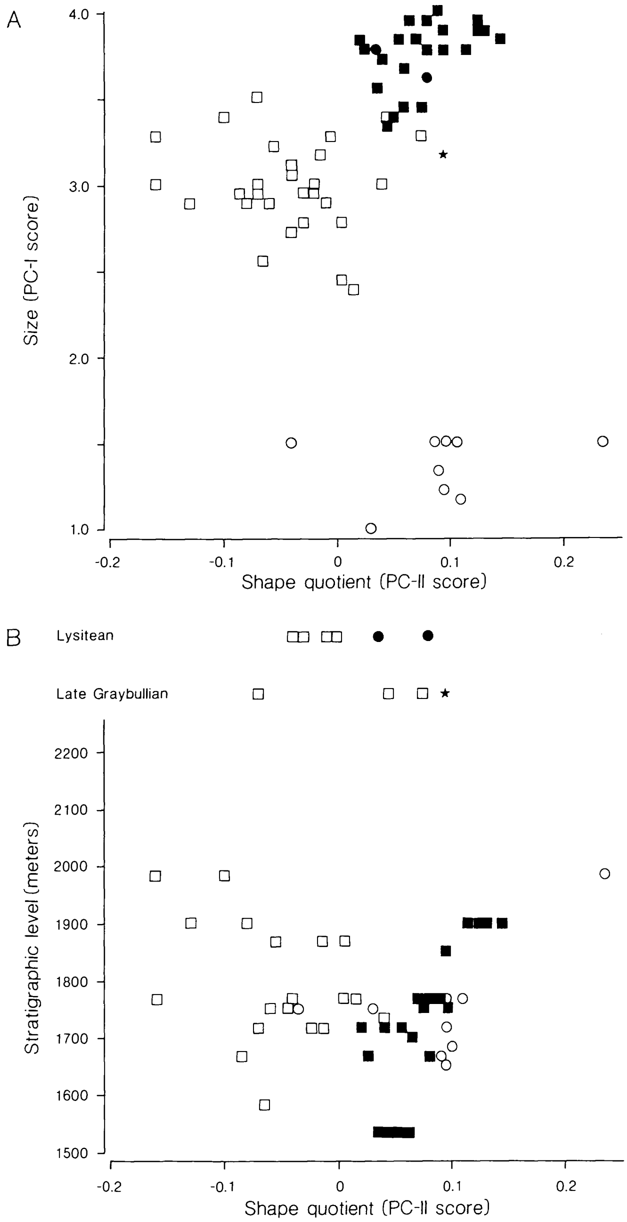

FIG. 28— Comparison of size and shape of M_3 in early Eocene Hyaenodontidae. Abscissa in both plots is compound shape quotient (second principal component score, based on crown length, crown width, trigonid length, and trigonid width, and accounting for 71% of non-size variance). Ordinate in upper figure (A) is compound size (first principal component score, accounting for 98.7% of total variance). Ordinate in lower figure (B) is stratigraphic level in Clarks Fork Basin section (with late Graybullian and Lysitean specimens from the northern and central Bighorn Basin added). Each symbol represents an individual specimen. Symbols: *Arfia*, solid squares; *Prolimnocyon*, open circles; *Prototomus*, open squares; *Pyrocyon*, solid star; and *Tritemnodon?*, solid circles.

The first three components were found to have the following loadings:

	PC-I	PC-II	PC-III
Component	0.645	0.006	0.002
Percent total variance	98.7%	0.9%	0.3%
M_3L	0.49	0.10	-0.87
M_3W	0.50	-0.40	0.24
M_3TRL	0.50	0.78	0.37
M_3TRW	0.50	-0.48	0.23

Loadings of the same sign and magnitude indicate that PC-I scores provide a good compound estimate of overall size, and this explains 98.7% of the total variance. Loadings of PC-II contrast trigonid length with the two measures of width and PC-II scores provide a compound shape quotient accounting for 71% of remaining non-size variance. PC-III scores provide a different shape quotient accounting for 23% of non-size variance, and additional component scores would total only 6% of non-size variance.

Size and shape are plotted against each other in Figure 28A. Genera tend to occupy discrete parts of the size-shape space, reflecting their distinctiveness. Size and shape are independent of each other here because PC-II was computed to be orthogonal to PC-I.

Figure 28B shows how M_3 shape changed through time. *Arfia* and *Prolimnocyon* both developed relatively longer and narrower trigonids. *Prototomus* shows a slight tendency in this direction. If *Tritemnodon?* and *Pyrocyon* evolved from *Prototomus*, which is plausible given present evidence, then they too indicate trends in this direction.

EVOLUTION IN HYAENODONTIDAE

Evidence presented above, summarized in Figures 4, 19, 26, and 28B permits some generalization about evolutionary patterns in early Eocene Hyaenodontidae:

1. Some species, like *Acarictis ryani*, *Galecyon mordax*, or *Prototomus deimos* exhibit short stratigraphic ranges, during which they changed little if any in form.
2. Some lineages, like the sequence from *Arfia zele* to *Arfia shoshoniensis* to *Arfia opisthotoma*, changed gradually through anagenesis at variable rates with no overlap of species in time that would indicate accompanying cladogenesis. Species can change without any evidence of branching. Anagenesis here involved shape as well as size, and the two did not necessarily change in concert.
3. Some species pairs, like *Prolimnocyon haematus* and *Prolimnocyon atavus* exhibit a "punctuated" pattern of abrupt replacement of one species by another, overlapping sufficiently in time to indicate that cladogenesis was involved— this was not simply the result of rapid morphological change in a single lineage.
4. In one case, divergence of *Prototomus martis* from *Prototomus phobos*, it appears that cladogenic branching is recorded. Here, as in *Cantius* and *Hyopsodus* (Gingerich, 1976) and in *Plesiadapis* (Gingerich, 1976b), the larger of the new sister species is the more common for a time after branching.

These observed patterns can all be explained by gradual evolution at rates varying from zero to a few darwins.

Hyaenodontidae are unknown in North America before the beginning of the Wasatchian land-mammal age, and hyaenodontids are one of the distinctive groups of mammals whose appearance marks the beginning of Wasatchian time. Evidence from the Clarks Fork Basin, where the early Wasatchian is best documented, shows that not one but six lineages of Hyaenodontidae are present when the family makes its first appearance. This, with coincident first appearances of other groups, appears to indicate that the family evolved elsewhere. Hyaenodontids certainly originated and diversified outside the Clarks Fork Basin, and they probably originated and diversified somewhere outside North America. Here it is worth noting that *all* carnivorous terrestrial mammals known from the late Eocene and Oligocene of Africa are hyaenodontid creodonts. There are no true Carnivora and there are no oxyaenid creodonts. The diversity and dominance of hyaenodontids in the early Cenozoic fauna of Africa makes it likely that Africa was their center of origin.

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TABLE 2 — Measurements of upper and lower cheek teeth of *Acarictis ryani*, new genus and species, from the Willwood Formation of the Clarks Fork Basin, Wyoming. Specimens included here are all early Wasatchian in age (1590 - 1700 meter interval in measured stratigraphic section). Measurements are defined in Figure 1. All measurements in mm. Asterisk indicates estimate.

Tooth position	UM 75805		UM 79081 (holotype)		UM 80195		UM 86291	
	L	W	L	W	L	W	L	W
Upper dentition								
P^3	--	--	--	--	--	--	3.7*	2.6
Lower dentition								
P_2	--	--	--	1.5	--	--	--	--
P_3	--	--	--	--	--	--	3.9	1.6
P_4	--	--	--	--	--	--	4.1*	1.9
M_1	--	--	3.9	2.2	--	--	--	1.5*
M_2	4.1*	2.6*	4.3*	2.6*	4.2*	2.7*	--	2.9*
Mandibular depth	6.4		5.8		6.7		6.3	

TABLE 3 — Measurements of upper and lower cheek teeth of the holotype of *Arfia zele*, new species, UM 69372 from the Willwood Formation of the Clarks Fork Basin, Wyoming. This specimen is early Wasatchian in age (middle Sandcouleean). Measurements are defined in Figure 1. All measurements in mm.

Upper dentition	L	W	H	Lower dentition	L	W	H
P^4	--	--		P_4	8.6	3.8	
M^1	--	--		M_1	6.1	3.5	
M^2	--	--		M_2	7.3	4.3	
M^3	--	--		M_3	8.0	4.7	

M_3 TRL = 4.7 M_3 TRW = 4.7 M_3 TRH = -- Mand. depth = 14.0

TABLE 4 — Summary of measurements of the upper and lower cheek teeth of *Arfia zele*, new species, from the Willwood Formation of the Clarks Fork Basin, Wyoming. Specimens included here are all early Wasatchian in age (1530 - 1570 meter interval in measured stratigraphic section). Measurements are defined in Figure 1. N = sample size, OR = observed range, $\bar{x}$ = mean, S = standard deviation, V = coefficient of variation. All measurements in mm.

Tooth position		*N*	*OR*	$\bar{x}$	*S*	*V*
Upper dentition						
	L	3	5.6 - 7.5	6.43	0.97	15.1
C^1	W	3	3.9 - 4.7	4.30	0.40	9.3
	H	--	--	--	--	--
P^3	L	4	6.6 - 7.6	7.08	0.46	6.5
	W	4	3.7 - 4.9	4.15	0.54	13.1
P^4	L	3	6.9 - 7.7	7.17	0.46	6.4
	W	2	6.0 - 6.4	6.20	0.28	4.6
M^1	L	3	6.3 - 6.7	6.47	0.21	3.2
	W	2	6.8 - 7.1	6.95	0.21	3.1
M^2	L	--	--	--	--	--
	W	1	9.7	--	--	--
M^3	L	1	6.4	--	--	--
	W	--	--	--	--	--
Lower dentition						
	L	1	5.5	--	--	
C_1	W	1	4.1	--	--	--
	H	1	12.5	--	--	--
P_1	L	--	--	--	--	--
	W	1	2.2	--	--	--
P_2	L	2	6.2 - 6.7	6.45	0.35	5.5
	W	2	3.2 - 3.6	3.40	0.28	8.3
P_3	L	3	6.9 - 7.6	7.33	0.38	5.2
	W	3	2.9 - 3.8	3.43	0.47	13.8
P_4	L	6	6.9 - 8.6	7.73	0.58	7.4
	W	6	3.6 - 4.1	3.87	0.18	4.5
M_1	L	5	6.1 - 6.8	6.54	0.27	4.1
	W	7	3.5 - 4.2	3.87	0.25	6.5
M_2	L	9	7.2 - 8.5	7.97	0.47	5.9
	W	10	4.3 - 5.0	4.66	0.25	5.4
M_3	L	6	8.0 - 9.5	8.82	0.58	6.6
	W	6	4.7 - 5.4	5.10	0.30	5.9
	TRL	7	4.7 - 5.5	5.01	0.27	5.5
	TRW	7	4.7 - 5.4	5.00	0.27	5.4
	TRH	2	8.5	--	--	--
Mandibular depth		4	13.8 - 15.8	14.80	1.05	7.1
Ln (L × W) of M_1		5	3.06 - 3.35	3.25	0.112	--
Ln (L × W) of M_2		9	3.45 - 3.71	3.61	0.104	--
Ln (L × W) of M_3		6	3.63 - 3.94	3.80	0.125	--
M_3 Trigonid L/W		7	0.96 - 1.02	1.00	0.021	--

TABLE 5 — Summary of measurements of the upper and lower cheek teeth of *Arfia shoshoniensis* (Matthew, 1915) from the Willwood Formation of the Clarks Fork Basin, Wyoming. Specimens included here are all early to middle Wasatchian in age (1645 - 1780 meter interval in measured stratigraphic section). Measurements are defined in Figure 1. Abbreviations as in Table 3. All measurements in mm.

Tooth position		*N*	*OR*	$\bar{x}$	*S*	*V*
Upper dentition						
	L	4	7.0 - 8.2	7.85	0.57	7.3
C^1	W	4	5.1 - 5.3	5.25	0.10	1.9
	H	2	14.8 - 17.1	15.95	1.63	10.2
P^2	L	1	8.4	--	--	--
	W	2	3.7 - 4.4	4.05	0.49	12.2
P^3	L	5	8.8 - 9.9	9.28	0.53	5.7
	W	6	4.6 - 5.8	5.13	0.44	8.6
P^4	L	7	8.1 - 9.7	8.70	0.54	6.2
	W	6	7.3 - 9.3	8.42	0.68	8.1
M^1	L	12	6.8 - 8.1	7.45	0.41	5.6
	W	11	7.6 - 9.0	8.37	0.42	5.1
M^2	L	6	8.3 - 10.8	9.68	0.97	10.0
	W	8	9.6 - 11.7	10.64	0.72	6.7
M^3	L	2	5.1 - 6.4	5.75	0.92	16.0
	W	2	12.8	--	--	--
Lower dentition						
	L	10	5.8 - 8.3	7.06	0.77	11.0
C_1	W	10	4.0 - 6.2	5.13	0.68	13.3
	H	--	--	--	--	--
P_1	L	4	3.8 - 4.7	4.23	0.38	8.9
	W	4	2.2 - 2.6	2.45	0.17	7.1
P_2	L	9	6.3 - 8.2	7.27	0.51	7.1
	W	9	3.4 - 4.1	3.79	0.23	6.3
P_3	L	10	8.0 - 9.5	8.49	0.43	5.0
	W	13	3.7 - 4.5	4.13	0.22	5.4
P_4	L	20	7.8 - 10.0	9.11	0.57	6.2
	W	19	4.1 - 4.8	4.58	0.18	4.1
M_1	L	24	6.6 - 8.5	7.32	0.42	5.7
	W	28	4.2 - 4.9	4.53	0.23	5.1
M_2	L	33	8.2 - 10.2	9.05	0.50	5.5
	W	41	4.8 - 5.7	5.22	0.24	4.5
M_3	L	14	9.1 - 11.5	10.41	0.72	6.9
	W	23	4.9 - 6.4	5.76	0.40	7.0
	TRL	19	4.9 - 6.6	5.83	0.44	7.5
	TRW	19	4.7 - 6.4	5.71	0.41	7.2
	TRH	11	9.0 - 10.8	10.12	0.58	5.7
Mandibular depth		28	13.8 - 22.0	17.76	2.35	13.2
Ln (L × W) of M_1		24	3.35 - 3.73	3.490	0.101	--
Ln (L × W) of M_2		33	3.67 - 4.04	3.853	0.088	--
Ln (L × W) of M_3		14	3.81 - 4.24	4.073	0.139	--
M_3 Trigonid L/W		19	0.97 - 1.08	1.023	0.034	--

TABLE 6 — Summary of measurements of the upper and lower cheek teeth of *Arfia opisthotoma* (Matthew, 1901) from the Willwood Formation of the Clarks Fork Basin, Wyoming. Specimens included here are all middle Wasatchian in age (1815 - 1970 meter interval in measured stratigraphic section). Measurements are defined in Figure 1. Abbreviations as in Table 3. All measurements in mm.

Tooth position		*N*	*OR*	$\bar{x}$	*S*	*V*
Upper dentition						
	L	1	7.9	--	--	--
C^1	W	1	5.7	--	--	--
	H	1	19.3	--	--	--
P^1	L	1	5.8	--	--	--
	W	1	2.5	--	--	--
P^2	L	2	7.9 - 8.2	8.05	0.21	2.64
	W	2	3.7 - 3.8	3.75	0.07	1.89
P^3	L	2	9.3 - 9.6	9.45	0.21	2.64
	W	2	5.5 - 5.9	5.70	0.28	4.96
P^4	L	3	9.2 - 9.8	9.50	0.30	3.16
	W	3	8.5 - 9.8	9.07	0.67	7.34
M^1	L	6	7.3 - 8.8	7.98	0.59	7.41
	W	7	8.1 - 9.6	8.73	0.64	7.36
M^2	L	3	10.8 - 11.7	11.17	0.47	4.23
	W	4	9.8 - 12.0	10.98	1.05	9.54
Lower dentition						
	L	2	7.3	--	--	--
C_1	W	2	4.7 - 5.3	5.00	0.42	8.49
	H	-	--	--	--	--
P_1	L	1	5.2	--	--	--
	W	2	2.5 - 2.7	2.60	0.14	5.44
P_2	L	4	7.3 - 8.3	7.78	0.46	5.88
	W	4	3.7 - 4.0	3.90	0.14	3.63
P_3	L	7	8.2 - 9.1	8.73	0.29	3.29
	W	8	3.9 - 4.6	4.28	0.21	4.96
P_4	L	13	8.7 - 10.5	9.24	0.44	4.73
	W	13	4.3 - 5.2	4.67	0.31	6.74
M_1	L	15	6.7 - 8.4	7.55	0.47	6.21
	W	15	4.2 - 5.0	4.61	0.21	4.55
M_2	L	9	8.6 - 9.6	9.23	0.32	3.47
	W	12	4.9 - 5.9	5.43	0.26	4.79
M_3	L	7	10.3 - 11.5	10.97	0.38	3.48
	W	8	5.3 - 6.0	5.76	0.26	4.54
	TRL	7	5.4 - 6.6	6.17	0.40	6.53
	TRW	7	5.1 - 6.0	5.61	0.31	5.58
	TRH	3	9.0 - 10.6	9.87	0.81	8.19
Mandibular depth		12	16.1 - 22.6	18.78	1.99	10.61
Ln (L × W) of M_1		15	3.37 - 3.74	3.55	0.102	--
Ln (L × W) of M_2		9	3.74 - 4.04	3.91	0.082	--
Ln (L × W) of M_3		7	4.07 - 4.22	4.16	0.061	--
M_3 Trigonid L/W		7	1.06 - 1.13	1.10	0.026	--

TABLE 7 — Measurements of upper and lower cheek teeth of the holotype of *Prototomus deimos*, new species, UM 79612 from the Willwood Formation of the Clarks Fork Basin, Wyoming. This specimen is middle Wasatchian in age (early Graybullian). Measurements are defined in Figure 1. All measurements in mm. Asterisk indicates estimate.

Upper dentition	L	W	H	Lower dentition	L	W	H
P^1	--	--		P_1	2.3	0.9	
P^2	--	--		P_2	3.9	1.3	
P^3	--	--		P_3	--	--	
P^4	--	--		P_4	5.1	2.0	
M^1	--	--		M_1	4.4	2.2	
M^2	--	--		M_2	5.1	3.2	
M^3	--	--		M_3	5.3	2.9	

M_3 TRL = 2.7 M_3 TRW = 2.8 M_3 TRH = 5.5 Mand. depth = 7.4

TABLE 8 — Summary of measurements of the upper and lower cheek teeth of *Prototomus deimos*, new species, from the Willwood Formation of the Clarks Fork Basin, Wyoming. Specimens included here are all early to middle Wasatchian in age (1540 - 1760 meter interval in measured stratigraphic section). Measurements are defined in Figure 1. Abbreviations as in Table 3. All measurements in mm.

Tooth position	*N*	*OR*	$\bar{x}$	*S*	*V*
Upper dentition					
M^1 L	2	4.3 - 4.4	4.35	0.07	1.63
W	2	5.1	--	--	--
M^2 L	1	5.3	--	--	--
W	1	7.0	--	--	--
Lower dentition					
P_1 L	1	2.3	--	--	--
W	1	0.9	--	--	--
P_2 L	2	3.9 - 4.0	3.95	0.07	1.79
W	3	1.3 - 1.5	1.37	0.12	8.39
P_3 L	1	5.2	--	--	--
W	1	1.6	--	--	--
P_4 L	2	5.1 - 5.4	5.25	0.21	4.04
W	3	1.9 - 2.1	0.22	0.10	5.00
M_1 L	4	4.4 - 4.9	4.58	0.24	5.15
W	4	2.2 - 2.6	2.45	0.19	7.80
M_2 L	4	5.0 - 5.3	5.13	0.13	2.44
W	5	3.1 - 3.6	3.36	0.23	6.85
M_3 L	5	5.0 - 5.6	5.34	0.26	4.87
W	5	2.9 - 3.3	3.02	0.18	5.93
TRL	3	2.7 - 2.8	2.73	0.06	2.08
TRW	3	2.8 - 3.2	2.97	0.21	7.03
TRH	1	5.5	--	--	--
Mandibular depth	4	7.4 - 9.9	8.42	1.13	13.30
Ln (L × W) of M_1	4	2.27 - 2.54	2.41	0.12	--
Ln (L × W) of M_2	4	2.79 - 2.95	2.86	0.08	--
Ln (L × W) of M_3	5	2.67 - 2.92	2.78	0.09	--
M_3 Trigonid L/W	3	0.87 - 0.96	0.92	0.05	--

TABLE 9 — Measurements of upper and lower cheek teeth of the holotype of *Prototomus phobos*, new species, YPM-PU 13019 from the Willwood Formation of the Bighorn Basin, Wyoming. This specimen is middle Wasatchian in age (Graybullian). Measurements are defined in Figure 1. All measurements in mm.

Upper dentition	L	W	H	Lower dentition	L	W	H
I^1	1.0	1.1		I_1	--	--	
I^2	1.0	1.2		I_2	--	--	
I^3	--	--		I_3	--	--	
C^1	--	--	--	C_1	3.4	2.4	--
P^1	3.0	1.1		P_1	2.7	0.9	
P^2	4.1	1.6		P_2	4.1	1.5	
P^3	4.5	2.0		P_3	5.1	1.6	
P^4	5.4	3.6		P_4	5.4	2.3	
M^1	5.3	5.2		M_1	4.8	2.8	
M^2	6.4	7.0		M_2	5.7	3.9	
M^3	3.7	6.9		M_3	6.2	3.7	

M_3 TRL = 3.3 M_3 TRW = 3.6 M_3 TRH = 5.9 Mand. depth = 9.4

TABLE 10 — Summary of measurements of the upper and lower cheek teeth of *Prototomus phobos*, new species, from the Willwood Formation of the Clarks Fork Basin, Wyoming. Specimens included here are all early to middle Wasatchian in age (1540 - 2110 meter interval in measured stratigraphic section). Measurements are defined in Figure 1. Abbreviations as in Table 3. All measurements in mm.

Tooth position		*N*	*OR*	$\bar{x}$	*S*	*V*
Upper dentition						
P^1	L	1	3.0	--	--	--
	W	1	1.1	--	--	--
P^2	L	1	4.1	--	--	--
	W	1	1.6	--	--	--
P^3	L	1	4.5	--	--	--
	W	1	2.0	--	--	--
P^4	L	7	5.4 - 6.5	5.86	0.42	7.16
	W	6	3.6 - 5.0	4.15	0.54	13.18
M^1	L	10	5.3 - 6.8	6.10	0.58	9.42
	W	11	5.2 - 6.8	5.95	0.51	8.64
M^2	L	9	5.5 - 7.3	6.49	0.52	7.95
	W	10	7.0 - 8.9	7.76	0.66	8.50
M^3	L	7	3.5 - 4.0	3.76	0.16	4.29
	W	7	6.9 - 8.7	7.60	0.57	7.45
Lower dentition						
	L	4	3.4 - 4.3	3.85	0.47	12.07
C_1	W	4	2.4 - 3.1	2.68	0.30	11.16
	H	--	--	--	--	--
P_1	L	1	2.7	--	--	--
	W	1	0.9	--	--	--
P_2	L	3	4.0 - 4.4	4.17	0.21	5.00
	W	3	1.4 - 1.6	1.50	0.10	6.67
P_3	L	6	4.8 - 5.8	5.28	0.42	7.90
	W	8	1.5 - 2.0	1.76	0.17	9.60
P_4	L	9	5.3 - 6.3	5.90	0.38	6.51
	W	9	2.1 - 2.4	2.29	0.15	6.33
M_1	L	11	4.8 - 6.0	5.35	0.34	6.45
	W	13	2.6 - 3.6	2.91	0.28	9.76
M_2	L	13	5.7 - 6.7	6.24	0.25	4.05
	W	15	3.8 - 4.5	4.06	0.22	5.32
M_3	L	13	5.3 - 7.2	6.37	0.54	8.45
	W	14	2.8 - 4.3	3.71	0.44	11.81
	TRL	10	3.2 - 3.8	3.36	0.18	5.30
	TRW	9	3.4 - 4.1	3.82	0.26	6.91
	TRH	5	5.8 - 6.8	6.18	0.39	6.31
Mandibular depth		16	8.8 - 13.0	10.78	1.23	11.43
Ln (L × W) of M_1		11	2.58 - 2.95	2.72	0.13	--
Ln (L × W) of M_2		13	3.10 - 3.31	3.21	0.06	--
Ln (L × W) of M_3		12	2.70 - 3.43	3.15	0.20	--
M_3 Trigonid L/W		9	0.78 - 0.97	0.88	0.06	--

TABLE 11 — Measurements of upper and lower cheek teeth of the holotype of *Prototomus martis*, new species, UM 87317 from the Willwood Formation of the Bighorn Basin, Wyoming. This specimen is middle Wasatchian in age (early Graybullian). Measurements are defined in Figure 1. All measurements in mm.

Upper dentition	L	W	H	Lower dentition	L	W	H
C^1	--	--	--	C_1	4.1	2.5	--
P^2	--	--		P_2	--	--	
P^3	--	--		P_3	--	--	
P^4	--	--		P_4	--	2.8	
M^1	--	--		M_1	6.4	3.5	
M^2	--	--		M_2	7.4	4.7	
M^3	--	--		M_3	7.0	4.3	

M_3 TRL = 3.8 M_3 TRW = 4.2 M_3 TRH = 7.0   Mand. depth = 11.5

TABLE 12 — Summary of measurements of the upper and lower cheek teeth of *Prototomus martis*, new species, from the Willwood Formation of the Clarks Fork Basin, Wyoming. Specimens included here are all early to middle Wasatchian in age (1690 - 1915 meter interval in measured stratigraphic section). Measurements are defined in Figure 1. Abbreviations as in Table 3. All measurements in mm.

Tooth position	*N*	*OR*	$\bar{x}$	*S*	*V*
Upper dentition					
C^1 L	2	4.1 - 4.6	4.35	0.35	8.13
W	2	3.4 - 4.0	3.70	0.42	11.47
P^1 L	1	3.7	--	--	--
P^2 L	1	5.9	--	--	--
W	--	--	--	--	--
P^3 L	1	6.2	--	--	--
W	--	--	--	--	--
P^4 L	1	6.9	--	--	--
W	1	5.2	--	--	--
M^1 L	6	5.9 - 6.8	6.55	0.36	5.44
W	5	6.3 - 7.4	6.68	0.47	6.98
M^2 L	5	6.4 - 7.3	6.88	0.34	4.97
W	4	7.8 - 9.0	8.43	0.61	7.28
M^3 L	3	4.1 - 4.5	4.23	0.23	5.46
W	2	8.2 - 8.4	8.30	0.14	1.70
Lower dentition					
C_1 L	5	3.6 - 4.9	4.24	0.47	11.13
W	5	2.5 - 3.4	3.04	0.35	11.55
P_1 L	1	2.6	--	--	--
W	1	1.6	--	--	--
P_2 L	1	5.5	--	--	--
W	2	1.7 - 2.2	1.95	0.35	18.13
P_3 L	6	5.6 - 6.8	6.25	0.42	6.69
W	9	2.0 - 2.7	2.31	0.26	11.13
P_4 L	11	5.8 - 7.6	6.52	0.55	8.48
W	12	2.5 - 3.3	2.86	0.28	9.83
M_1 L	15	5.4 - 7.2	6.25	0.55	8.80
W	15	3.0 - 4.0	3.43	0.28	8.22
M_2 L	13	6.4 - 8.0	7.08	0.46	6.53
W	16	4.2 - 5.2	4.73	0.28	5.86
M_3 L	12	6.7 - 8.7	7.34	0.55	7.47
W	14	3.8 - 5.5	4.32	0.48	11.09
TRL	11	3.4 - 4.0	3.75	0.21	5.39
TRW	11	3.7 - 4.9	4.17	0.37	8.85
TRH	10	5.8 - 8.1	7.04	0.68	9.70
Mandibular depth	17	10.1 - 16.0	12.46	1.90	15.32
Ln (L × W) of M_1	12	2.79 - 3.36	3.08	0.18	--
Ln (L × W) of M_2	13	3.36 - 3.67	3.51	0.10	--
Ln (L × W) of M_3	11	3.29 - 3.87	3.46	0.17	--
M_3 Trigonid L/W	11	0.78 - 0.97	0.90	0.05	--

TABLE 13 — Summary of measurements of the upper and lower cheek teeth of *Prototomus secundarius* Cope, 1875, from the Willwood Formation of the Bighorn Basin, Wyoming. Specimens included here are all middle to late Wasatchian (late Graybullian and Lysitean) in age. Measurements are defined in Figure 1. Abbreviations as in Table 3. All measurements in mm.

Tooth position	*N*	*OR*	$\bar{x}$	*S*	*V*
Upper dentition					
M^2 L	1	6.8	--	--	--
W	1	8.0	--	--	--
M^3 L	1	4.5	--	--	--
W	1	8.0	--	--	--
Lower dentition					
L	2	3.8 - 4.1	3.95	0.21	5.37
C_1 W	2	2.5 - 2.7	2.60	0.14	5.42
H	--	--	--	--	--
P_3 L	2	5.2 - 5.5	5.35	0.21	3.96
W	2	1.8 - 2.0	1.90	0.14	7.42
P_4 L	4	6.0 - 7.1	6.63	0.56	8.48
W	6	2.5 - 3.1	2.70	0.23	8.44
M_1 L	3	6.2 - 6.6	6.33	0.23	3.65
W	5	3.0 - 3.6	3.24	0.23	7.10
M_2 L	4	6.7 - 7.2	6.95	0.21	2.99
W	6	4.0 - 4.8	4.30	0.28	6.42
M_3 L	5	6.5 - 7.1	6.82	0.24	3.51
W	5	3.5 - 4.0	3.82	0.22	5.71
TRL	4	3.1 - 3.5	3.38	0.19	5.64
TRW	4	3.5 - 4.1	3.80	0.26	6.79
TRH	2	6.7	--	--	--
Mandibular depth	4	10.30 - 14.00	12.58	1.60	12.67
Ln (L × W) of M_1	3	2.96 - 3.17	3.04	0.11	--
Ln (L × W) of M_2	4	3.33 - 3.54	3.41	0.09	--
Ln (L × W) of M_3	5	3.12 - 3.33	3.26	0.08	--
M_3 Trigonid L/W	4	0.85 - 0.95	0.89	0.04	--

TABLE 14 — Summary of measurements of the upper and lower cheek teeth of *Prototomus robustus* (Matthew, 1915) from the Willwood Formation of the Bighorn and Clarks Fork basins, Wyoming. Specimens included here are all middle Wasatchian in age (middle to late Graybullian). Measurements are defined in Figure 1. Abbreviations as in Table 3. All measurements in mm.

Tooth position		*N*	*OR*	$\bar{x}$	*S*	*V*
Upper dentition						
	L	1	6.3	--	--	--
C^1	W	1	4.5	--	--	--
	H	--	--	--	--	--
M^1	L	2	6.8 - 7.4	7.10	0.42	5.97
	W	2	6.9 - 8.2	7.55	0.92	12.17
M^2	L	2	7.3 - 7.9	7.60	0.42	5.58
	W	2	9.5 - 9.9	9.70	0.28	2.91
M^3	L	1	3.9	--	--	--
	W	1	8.8	--	--	--
Lower dentition						
	L	1	5.2	--	--	--
C_1	W	1	3.8	--	--	--
	H	--	--	--	--	--
P_2	L	1	5.7	--	--	--
	W	1	2.2	--	--	--
P_3	L	1	6.5	--	--	--
	W	1	3.4	--	--	--
P_4	L	7	7.1 - 7.9	7.59	0.27	3.52
	W	9	3.1 - 4.1	3.60	0.32	9.00
M_1	L	7	6.2 - 7.0	6.71	0.32	4.74
	W	8	3.5 - 4.2	3.95	0.23	5.87
M_2	L	9	7.3 - 8.3	7.91	0.37	4.70
	W	12	4.9 - 5.7	5.30	0.24	4.47
M_3	L	7	6.9 - 9.2	8.01	0.75	9.33
	W	7	4.2 - 5.3	4.97	0.40	8.01
	TRL	5	4.2 - 4.8	4.48	0.26	5.78
	TRW	5	4.4 - 5.1	4.82	0.30	6.29
	TRH	3	7.7 - 9.0	8.17	0.72	8.85
Mandibular depth		7	11.2 - 18.9	15.10	3.05	20.22
Ln (L × W) of M_1		7	3.14 - 3.38	3.27	0.09	--
Ln (L × W) of M_2		9	3.62 - 3.86	3.73	0.07	--
Ln (L × W) of M_3		7	3.37 - 3.89	3.68	0.17	--
M_3 Trigonid L/W		5	0.84 - 1.07	0.93	0.11	--

TABLE 15 — Summary of measurements of the upper and lower cheek teeth of *Tritemnodon? strenuus* (Cope, 1875) from the Willwood Formation of the Bighorn Basin, Wyoming. UM 21186 from the San Jose Formation of the San Juan Basin, New Mexico, is also included. Wyoming specimens are all late Wasatchian in age (Lysitean), while the New Mexico specimen may be either middle or late Wasatchian (late Graybullian or Lysitean). Measurements are defined in Figure 1. Abbreviations as in Table 3. All measurements in mm.

Tooth position	*N*	*OR*	$\bar{x}$	*S*	*V*
Upper dentition					
L	1	7.6	--	--	--
C^1 W	1	5.1	--	--	--
H	--	--	--	--	--
P^2 L	1	7.2	--	--	--
W	1	3.6			
P^3 L	1	8.5	--	--	--
W	1	5.5	--	--	--
M^1 L	1	9.4	--	--	--
W	1	10.2	--	--	--
M^3 L	1	5.0	--	--	--
W	1	11.3	--	--	--
Lower dentition					
P_2 L	1	7.3	--	--	--
W	2	3.0 - 3.2	3.10	0.14	4.55
P_4 L	2	8.4 - 9.0	8.70	0.42	4.87
W	3	3.8 - 4.3	4.10	0.26	6.46
M_1 L	3	7.8 - 8.2	7.97	0.21	2.60
W	3	4.6 - 5.1	4.77	0.29	6.06
M_2 L	2	8.4 - 10.0	9.20	1.13	12.28
W	2	5.7 - 6.1	5.90	0.28	4.80
M_3 L	5	8.2 - 10.8	9.52	1.07	11.20
W	5	5.3 - 6.4	5.90	0.48	8.22
TRL	3	5.6 - 5.9	5.70	0.17	3.04
TRW	3	4.5 - 5.9	5.20	0.70	13.46
TRH	2	9.3 - 11.2	10.25	1.34	13.11
Mandibular depth	3	19.3 - 21.0	20.13	0.85	4.23
Ln (L × W) of M_1	3	3.58 - 3.70	3.64	0.06	--
Ln (L × W) of M_2	2	3.87 - 4.11	3.99	0.17	--
Ln (L × W) of M_3	5	3.77 - 4.22	4.02	0.19	--
M_3 Trigonid L/W	3	1.00 - 1.24	1.11	0.12	--

TABLE 16 — Measurements of upper and lower cheek teeth of the holotype of *Pyrocyon dioctetus*, new genus and species, UM 94757 from the Willwood Formation of the Bighorn Basin, Wyoming. This specimen is middle Wasatchian in age (late Graybullian). Measurements are defined in Figure 1. All measurements in mm. Asterisk indicates estimate.

Upper dentition	L	W	H	Lower dentition	L	W	H
C^1	5.6	4.6	12.1	C_1	--	--	--
P^1	--	--		P_1	4.3	1.8	
P^2	--	--		P_2	6.2	2.8	
P^3	--	--		P_3	6.7	2.9	
P^4	--	--		P_4	6.9	3.5	
M^1	--	--		M_1	6.3	3.6	
M^2	7.2	8.9		M_2	7.1	4.4	
M^3	--	--		M_3	7.6	4.2	

M_3 TRL = 4.3 M_3 TRW = 4.0 M_3 TRH = 7.5 Mand. depth = 13.9

TABLE 17 — Summary of measurements of the lower cheek teeth of *Galecyon mordax* (Matthew, 1915) from the Willwood Formation of the Clarks Fork Basin, Wyoming. Specimens included here are all early or early middle Wasatchian in age (1560 - 1760 meter interval in measured stratigraphic section). Measurements are defined in Figure 1. Abbreviations as in Table 3. All measurements in mm.

Tooth position		*N*	*OR*	$\bar{x}$	*S*	*V*
Lower dentition						
P_4	L	1	5.9	--	--	--
	W	1	3.0	--	--	--
M_1	L	3	6.2 - 6.6	6.47	0.23	3.57
	W	3	3.5 - 3.9	3.67	0.21	5.67
M_2	L	3	6.4	6.40	--	--
	W	3	3.7 - 4.4	4.03	0.35	8.71
M_3	L	1	4.8	--	--	--
	W	2	2.7 - 4.0	3.35	0.92	27.43
Mandibular depth		2	9.5 - 13.8	11.65	3.04	26.10
Ln (L × W) of M_1		3	3.08 - 3.25	3.16	0.09	--
Ln (L × W) of M_2		3	3.16 - 3.34	3.25	0.09	--
Ln (L × W) of M_3		1	2.56	--	--	--

TABLE 18 — Measurements of upper and lower cheek teeth of the holotype of *Prolimnocyon haematus*, new species, UM 65622 from the Willwood Formation of the Clarks Fork Basin, Wyoming. This specimen is early Wasatchian in age (late Sandcouleean). Measurements are defined in Figure 1. All measurements in mm.

Upper dentition	L	W	H	Lower dentition	L	W	H
C^1	2.9	2.3	6.4	C_1	--	--	--
P^1	2.8	1.4		P_1	--	--	
P^2	4.0	1.7		P_2	--	--	
P^3	--	--		P_3	--	--	
P^4	5.0	3.8		P_4	4.4	2.0	
M^1	5.0	5.0		M_1	4.4	2.6	
M^2	4.8	6.1		M_2	4.8	3.0	
M^3	--	--		M_3	--	--	

M_3 TRL = -- M_3 TRW = -- M_3 TRH = -- Mand. depth = 7.1

TABLE 19 — Summary of measurements of the upper and lower cheek teeth of *Prolimnocyon haematus*, new species, from the Willwood Formation of the Clarks Fork Basin, Wyoming. Specimens included here are all early Wasatchian in age (1600 - 1760 meter interval in measured stratigraphic section). Measurements are defined in Figure 1. Abbreviations as in Table 3. All measurements in mm.

Tooth position		*N*	*OR*	$\bar{x}$	*S*	*V*
Upper dentition						
	L	1	2.9	--	--	--
C^1	W	1	2.3	--	--	--
	H	1	6.4	--	--	--
P^1	L	1	2.8	--	--	--
	W	1	1.4	--	--	--
P^2	L	1	4.0	--	--	--
	W	1	1.7	--	--	--
P^3	L	1	4.1	--	--	--
	W	1	1.6	--	--	--
P^4	L	2	4.6 - 5.0	4.80	0.28	5.90
	W	2	3.5 - 3.8	3.65	0.21	5.81
M^1	L	2	4.5 - 5.0	4.75	0.35	7.45
	W	2	4.5 - 5.0	4.75	0.35	7.45
M^2	L	1	4.8	--	--	--
	W	1	6.1	--	--	--
Lower dentition						
	L	1	3.1 - 3.7	3.40	0.42	12.47
C_1	W	2	2.2 - 2.4	2.30	0.14	6.13
	H	--	--	--	--	--
P_1	L	1	1.9	--	--	--
	W	1	1.1	--	--	--
P_2	L	5	3.5 - 3.7	3.62	0.08	2.29
	W	5	1.5 - 1.7	1.58	0.08	5.32
P_3	L	4	3.7 - 4.1	3.93	0.17	4.35
	W	3	1.5 - 1.7	1.60	0.10	6.25
P_4	L	8	4.3 - 5.0	4.60	0.28	6.15
	W	8	1.9 - 2.5	2.11	0.20	9.62
M_1	L	6	4.4 - 4.9	4.63	0.23	5.03
	W	9	2.3 - 3.3	2.63	0.27	10.42
M_2	L	11	4.4 - 5.3	4.92	0.27	5.51
	W	11	3.0 - 3.8	3.35	0.24	7.22
M_3	L	7	2.6 - 3.4	3.09	0.28	9.03
	W	9	1.5 - 1.9	1.66	0.15	9.10
	TRL	8	1.4 - 1.9	1.70	0.17	9.94
	TRW	9	1.4 - 1.9	1.62	0.17	10.61
	TRH	7	2.2 - 3.0	2.44	0.27	11.06
Mandibular depth		10	6.8 - 9.2	7.76	0.90	11.57
Ln (L × W) of M_1		5	2.40 - 2.58	2.49	0.08	--
Ln (L × W) of M_2		10	2.67 - 2.96	2.80	0.09	--
Ln (L × W) of M_3		7	1.36 - 1.81	1.64	0.18	--
M_3 Trigonid L/W		8	0.89 - 1.13	1.04	0.07	--

TABLE 20 — Summary of measurements of the upper and lower cheek teeth of *Prolimnocyon atavus* Matthew, 1915, from the Willwood Formation of the Bighorn and Clarks Fork basins, Wyoming. Specimens included here are all middle and late Wasatchian in age (Graybullian through Lysitean of Bighorn Basin; 1760 - 2110 meter interval in Clarks Fork Basin stratigraphic section). Measurements are defined in Figure 1. Abbreviations as in Table 3. All measurements in mm.

Tooth position	*N*	*OR*	$\bar{x}$	*S*	*V*
Upper dentition					
P^2 L	1	4.9	--	--	--
W	1	2.0	--	--	--
P^3 L	--	--	--	--	--
W	1	2.7			
P^4 L	3	5.6 - 6.6	6.10	0.50	8.20
W	3	4.6 - 5.6	5.23	0.55	10.52
M^1 L	4	5.4 - 6.8	5.87	0.66	11.24
W	4	5.6 - 7.0	6.30	0.70	11.11
M^2 L	3	3.8 - 4.8	4.37	0.51	11.74
W	3	7.5 - 8.8	7.93	0.75	9.47
M^3 L	1	1.9	--	--	--
W	--	--		--	--
Lower dentition					
P_2 L	1	4.2	--	--	--
W	1	2.0	--	--	--
P_3 L	1	5.0	--	--	--
W	1	2.1	--	--	--
P_4 L	3	4.8 - 6.1	5.47	0.65	11.90
W	4	2.5 - 2.7	2.55	0.10	3.92
M_1 L	5	5.2 - 6.2	5.60	0.43	7.68
W	6	3.0 - 3.6	3.15	0.23	7.43
M_2 L	11	5.0 - 6.2	5.48	0.34	6.26
W	13	3.4 - 4.0	3.64	0.16	4.42
M_3 L	5	2.7 - 3.3	3.00	0.28	9.43
W	5	1.4 - 1.9	1.72	0.19	11.16
TRL	2	1.9 - 2.1	2.00	0.14	7.05
TRW	2	1.6 - 1.8	1.70	0.14	8.29
TRH	2	2.6 - 2.8	2.70	0.14	5.24
Mandibular depth	9	7.2 - 10.1	8.87	0.87	9.84
Ln (L × W) of M_1	5	2.75 - 3.11	2.86	0.15	--
Ln (L × W) of M_2	11	2.89 - 3.21	3.00	0.09	--
Ln (L × W) of M_3	5	1.33 - 1.78	1.63	0.20	--
M_3 Trigonid L/W	2	1.06 - 1.31	1.18	0.18	--