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SYSTEMATICS OF PALEOCENE VIVERRAVIDAE (MAMMALIA, CARNIVORA) IN THE BIGHORN BASIN AND CLARK'S FORK BASIN, WYOMING

By

Philip D. Gingerich and Dale A. Winkler[1]

Abstract.—Four genera and ten species of Viverravidae are known in faunas representing the Torrejonian and Tiffanian land-mammal ages in the Bighorn and Clark's Fork basins, Wyoming. These are, in order of appearance: *Simpsonictis tenuis* (Simpson), *S. pegus* (n. sp.), *Bryanictis microlestes* (Simpson), and *Protictis haydenianus* Cope from the Torrejonian; *Raphictis gausion* (n. gen. and sp.), *Protictis paralus* Holtzman, and *P. agastor* (n. sp.) from the middle Tiffanian; and *Protictis laytoni* (n. sp.), *P. schaffi* (n. sp.), and *P. dellensis* (Dorr) from the late Tiffanian. Torrejonian "*Bryanictis*" *vanvaleni* (MacIntyre) from New Mexico and southern Wyoming is here placed in a new genus *Intyrictis*. Most Paleocene viverravids are represented by dental remains, but a compressed cranium of *Protictis schaffi* is known as well. The basicranium of this specimen preserves a canal medial to the petrosal interpreted to represent an inferior petrosal sinus, and grooves are preserved for both promontory and stapedial branches of the internal carotid artery. *Protictis* is one of five Torrejonian genera of Viverravidae known from North America. It is one of only two Tiffanian genera of Viverravidae. Paleocene *Protictis* may be the common ancestor of all known Eocene Viverravidae: *Protictis schaffi* is a likely ancestor for later *Viverravus*, and *Protictis dellensis* may be the ancestor of later *Didymictis*. Alternatively, *Didymictis* may be independently derived from *Bryanictis*.

INTRODUCTION

Viverravidae are the oldest members of the mammalian order Carnivora known in the fossil record, appearing in the early Paleocene and ranging through the middle and possibly late Eocene. It should be noted in this context that the late Cretaceous "miacid?" described by Russell (1962, 1975) is now regarded as marsupial rather than carnivoran (Clemens, 1966; Clemens et al., 1979). A single tooth representing the oldest viverravid has been described from Puercan (early Paleocene) strata of New Mexico (MacIntyre, 1966). Additional more complete specimens are known from transitional early-middle Paleocene strata in Utah. However the first real radiation of Viverravidae occurred during the Torrejonian Land-Mammal Age (middle Paleocene). A minimum of six species lineages belonging to five genera are present in North America during the Torrejonian, and four species lineages belonging to two genera are present during the Tiffanian

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Land-Mammal Age (late Paleocene). Viverravids are represented in the Paleocene of Asia, but they are not known from the Paleocene of Europe or South America. Consequently, North America and possibly Asia are likely centers of origin and evolution of Viverravidae. A second family of primitive Carnivora, Miacidae, appears in North America in the middle Clarkforkian (earliest Eocene; Rose, 1981; Gingerich, 1983b). Viverravids are more specialized than miacids in consistently lacking upper and lower third molars, teeth that are retained in early representatives of most modern families of Carnivora.

Viverravidae are sometimes linked to the origin of catlike aeluroid families of Carnivora (Felidae, Viverridae, and Hyaenidae) because of their reduced dental formula and other resemblances to more derived aeluroids (Matthew, 1909; Gregory and Hellman, 1939; Flynn and Galiano, 1982). However, there is little evidence of evolutionary continuity between Viverravidae, which radiated in the Paleocene and early Eocene, and any of the aeluroid families of Carnivora, which did not begin to diversify until the late Eocene or early Oligocene. We follow Flynn and Galiano (1982) in regarding Viverravidae as a family distinct from Miacidae, basing this distinction not on cladistic character analysis but rather on evidence of evolutionary independence of the two groups, interpreted in the context of their known geographic and stratigraphic distributions. Viverravidae are unlikely to be ancestral to any of the modern families of carnivores, but they are nevertheless an important component in many Paleocene mammalian faunas.

We shall outline the fossil record and evolutionary systematics of North American Viverravidae known from the Torrejonian and Tiffanian Land-Mammal Ages (middle and late Paleocene) in the northern part of the Western Interior. This review is not intended to be a full systematic revision of Paleocene viverravids, although we have necessarily compared new material to type and important reference samples of all known species. Samples compared here are referenced in the partial synonymy and the typodigm given for each species studied. New specimens are also listed as referred material. Most fossil specimens described here come from one of four major quarries: Rock Bench Quarry and Cedar Point Quarry in the northern Bighorn Basin, or Princeton Quarry and Schaff Quarry in the Clark's Fork Basin. All four of these quarries were discovered by members of Princeton University field parties working under the direction of Glenn L. Jepsen, and the major collection from each is housed in the Department of Geological and Geophysical Sciences at Princeton. New specimens described here provide the first reliable indication of viverravid diversity in the late Paleocene.

Virtually all systematic study of Viverravidae is based on dental remains. We here describe the first skull of a Paleocene viverravid preserving the basicranium essentially intact. Postcranial anatomy of *Protictis*, to the extent that this is known, was reviewed by MacIntyre (1966). The only adequate sample of dental remains of middle or late Paleocene Viverravidae reported previously comes from Gidley Quarry (Torrejonian) in the Crazy Mountain Basin, Montana (Simpson, 1935, 1937; MacIntyre, 1962, 1966). Other important papers on Paleocene Viverravidae include Cope (1882), Matthew (1937, actually written some years earlier), Dorr (1952), Holtzman (1978), Rigby (1980), and Flynn and Galiano (1982). Our principal objective in undertaking this review of Paleocene Viverravidae was to determine, if possible, how *Protictis* and its Paleocene allies might be related to early Eocene *Viverravus* and *Didymictis*, an objective requiring detailed comparative analysis of all transitional late Paleocene species. This study was aided immeasurably by extensive comments on carnivores and other middle and late Paleocene mammals published by Rose (1981).

The stratigraphic setting and temporal succession of Paleocene faunas in the Bighorn, Clark's Fork, and Crazy Mountain basins are discussed in Gingerich (1976, 1983a), Gingerich et al. (1980), Rose (1981), and Krause and Gingerich (1983). Zones of the Torrejonian and Tiffanian land-mammal ages are those developed by Gingerich (1976, 1983a). Dental and other anatomical nomenclature employed here follows MacIntyre (1966) and Van Valen (1966).

Measurements taken on upper and lower teeth are shown diagrammatically in Figure 1. All measurements are in millimeters. Fossil localities prefaced by FG or SC are University of Michigan localities in the Foster Gulch or Sand Coulee areas of the Bighorn and Clark's Fork basins, respectively. The following museum acronyms are used in the text and figures: AMNH, American Museum of Natural History, New York; SMM, Science Museum of Minnesota, St. Paul; UM, University of Michigan Museum of Paleontology, Ann Arbor; and USNM, National Museum of Natural History, Washington.

DENTAL VARIATION AND SEXUAL DIMORPHISM

Dental variation in carnivorous mammals is still not well studied. The only quantitative analyses of dental variation in large homogeneous samples of extant species are those by Gingerich and Winkler (1979) and Pengilly (1984), concerned with foxes of the genera *Vulpes* and *Alopex*, respectively. Conclusions applicable to this study are that upper and lower first molars are the least variable cheek teeth in the dentition of carnivores (as they generally are in other mammals), and that these teeth typically have a range of variation in linear dimensions of about 0.20 units on a natural logarithmic scale. Logarithmic scales of measurement are appropriate because we are interested in proportional rather than absolute differences between the largest and smallest specimens of a species. A typical range of variation in linear dimensions of M_1 (or M^1) of 0.20 units is, as expected, half that (0.40 units) characterizing variation in areal dimensions. In Figures 2, 3, and 4, a standard range of variation of 0.20 units is applied in interpreting linear measurements of teeth in quarry samples of Paleocene carnivores.

Extant foxes exhibit little sexual dimorphism in tooth size or mandibular morphology. However, some modern carnivores (e.g., *Martes* and *Mustela*) are markedly dimorphic, with males and females of the same species differing on average by about 0.20 units (i.e., there is little overlap in size between individuals of opposite sex, and sexes appear as paired "species" in simple graphs of dental or cranial variation). Linear measurements of central cheek teeth may, in highly dimorphic species, have coefficients of variation approaching 10, with the total range of variation of such linear measurements approaching 0.30-0.40 units on a logarithmic scale, almost double values expected in nondimorphic species.

Homogeneous samples of Paleocene species of Viverravidae are rarely large enough to test whether they include significant sexual dimorphism. Coefficients of variation of dental dimensions in *Protictis haydenianus* from middle Paleocene horizons in New Mexico (MacIntyre, 1966: tables 3-4), *Bryanictis microlestes* from Gidley Quarry, Montana (MacIntyre, 1966: tables 9-10, see also Table 3 in this paper), *Protictis paralus* (Table 5), and *P. schaffi* (Table 7) are similar to those reported for nondimorphic extant foxes. Graphs of dental measurements for quarry samples of these species, shown in Figures 2-4, exhibit no consistent pattern of pairing that would suggest marked dimorphism. Each can be accommodated within circles 0.20 units in diameter. However, two species, *Protictis agastor* and *P. dellensis*, appear to be more variable (see Tables 8 and 9). Circles 0.20 units in diameter are too small to contain dental measurements of these species (as graphed in Figures 3 and 4). We conservatively interpret this variability as indicating that *Protictis agastor* and *P. dellensis* are more dimorphic than other Viverravidae (alternatively, there may be two distinct species of large *Protictis* in the middle and late Tiffanian). On the basis of comparisons and measurements presented here, we suspect that most species of Viverravidae were only weakly dimorphic in body size and tooth size.

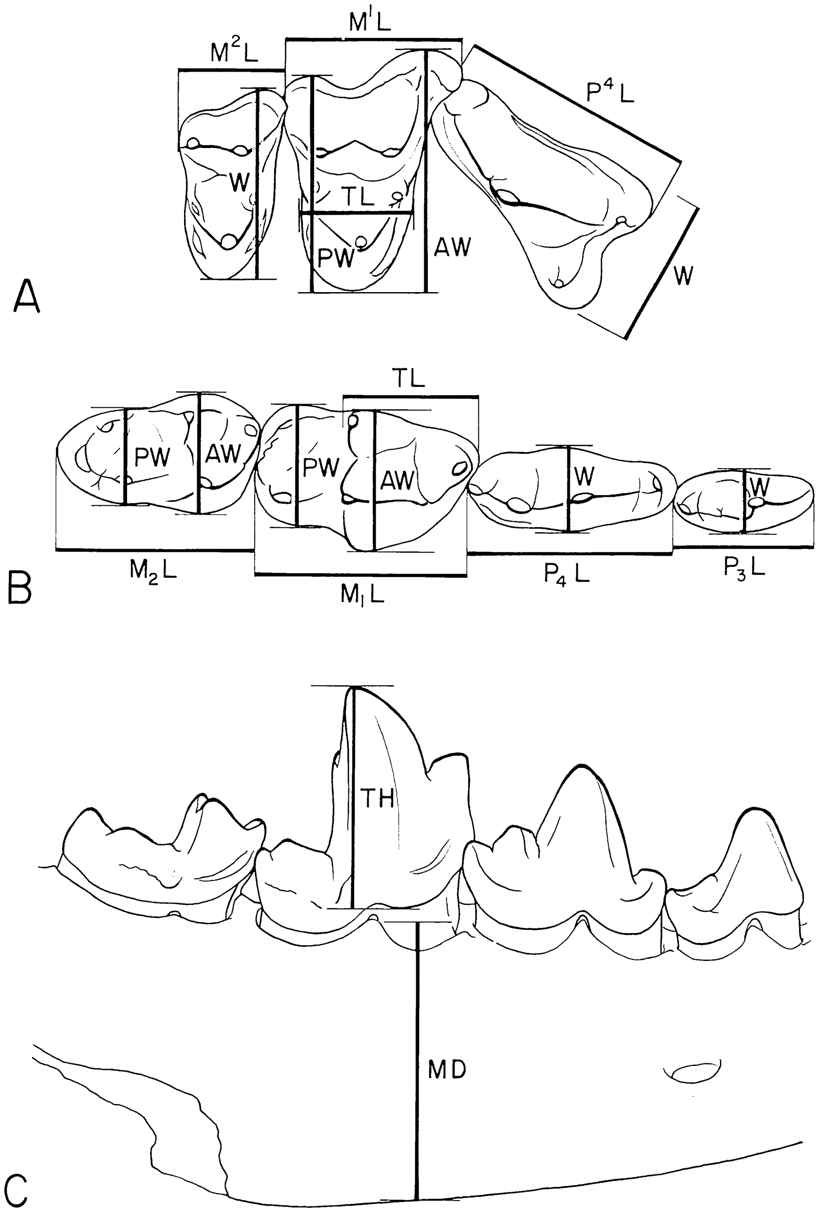


FIG. 1— Right maxillary and mandibular dentition of *Protictis schaffi*, showing measurements used in this study. A, upper premolar and molars in occlusal view. B, lower premolars and molars in occlusal view. C, lower premolars and molars in lateral view. *AW* = anterior width, *L* = length, *MD* = mandibular depth, *PW* = posterior width, *TH* = trigonid height, *TL* = trigon length (or trigonid length), and *W* = width. Canine length measured as maximum diameter at base of crown, canine width measured perpendicular to length at base of crown. Trigonid height of M_2 measured as shown for M_1. All measurements in millimeters.

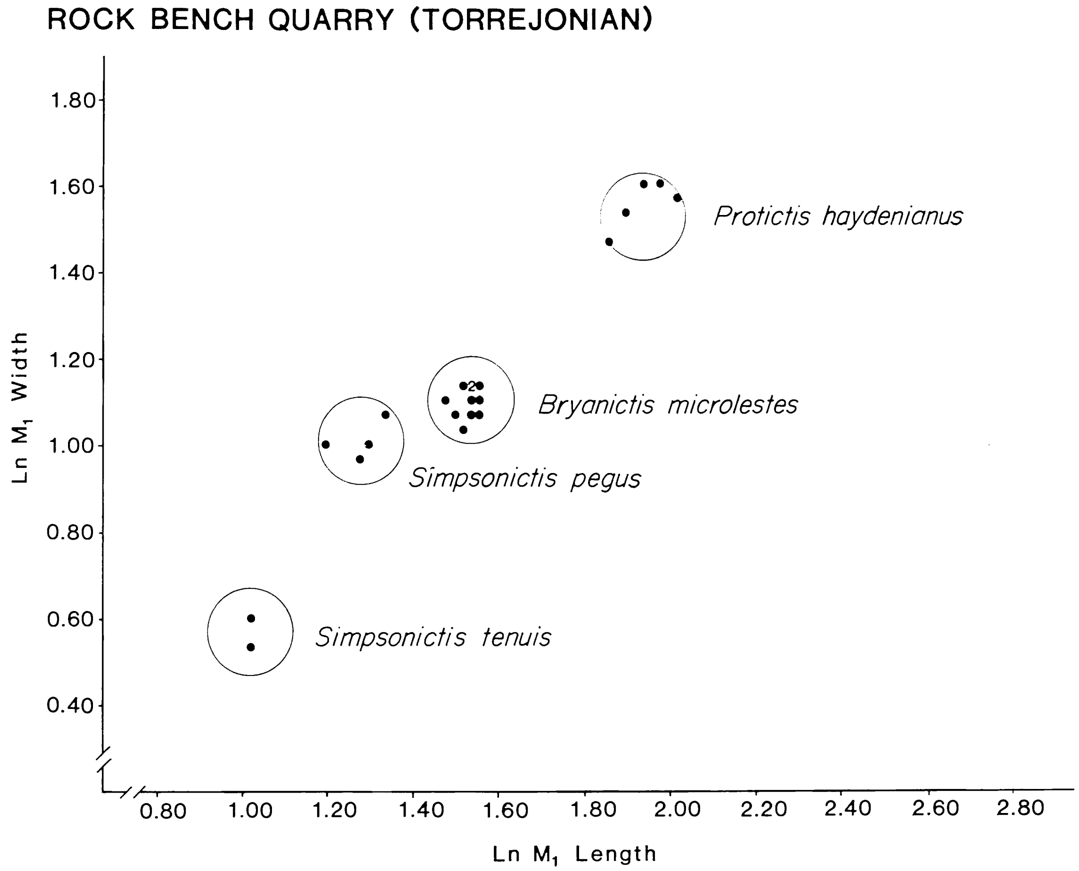


FIG. 2 – Bivariate scatter of natural logarithm of crown length and natural logarithm of crown width (anterior width) of viverravid first lower molars from Rock Bench Quarry, Torrejonian (middle Paleocene), in the northern Bighorn Basin, Wyoming. Logarithmically transformed axes make intraspecific variability of samples of large species comparable to those of small species. Four species are represented, as shown, each with an observed range of variation of about 0.20 units on the abscissa and ordinate. Note high correlation of molar length and width across all four species.

SYSTEMATIC PALEONTOLOGY

Pairwise comparison of middle and late Paleocene specimens of Viverravidae from Rock Bench, Cedar Point, Princeton, and Schaff quarries with each other and with specimens of later *Viverravus* and *Didymictis* served to demonstrate a wide range of morphological diversity within the family, but it did little to clarify species and evolutionary lineages (or taxonomic groups derived from these). For this purpose it proved advantageous to construct a series of simple bivariate phenetic diagrams for each of the three stratigraphic samples under study (Princeton and Schaff quarries were combined because they are at essentially the same stratigraphic level). This approach permitted clear separation of four species groups at Rock Bench Quarry (Fig. 2), three at Cedar Point Quarry (Fig. 3), and three at Princeton Quarry Schaff Quarry (Fig. 4). Unfortunately, the fragmentary nature of most specimens precluded meaningful multivariate morphometric comparison.

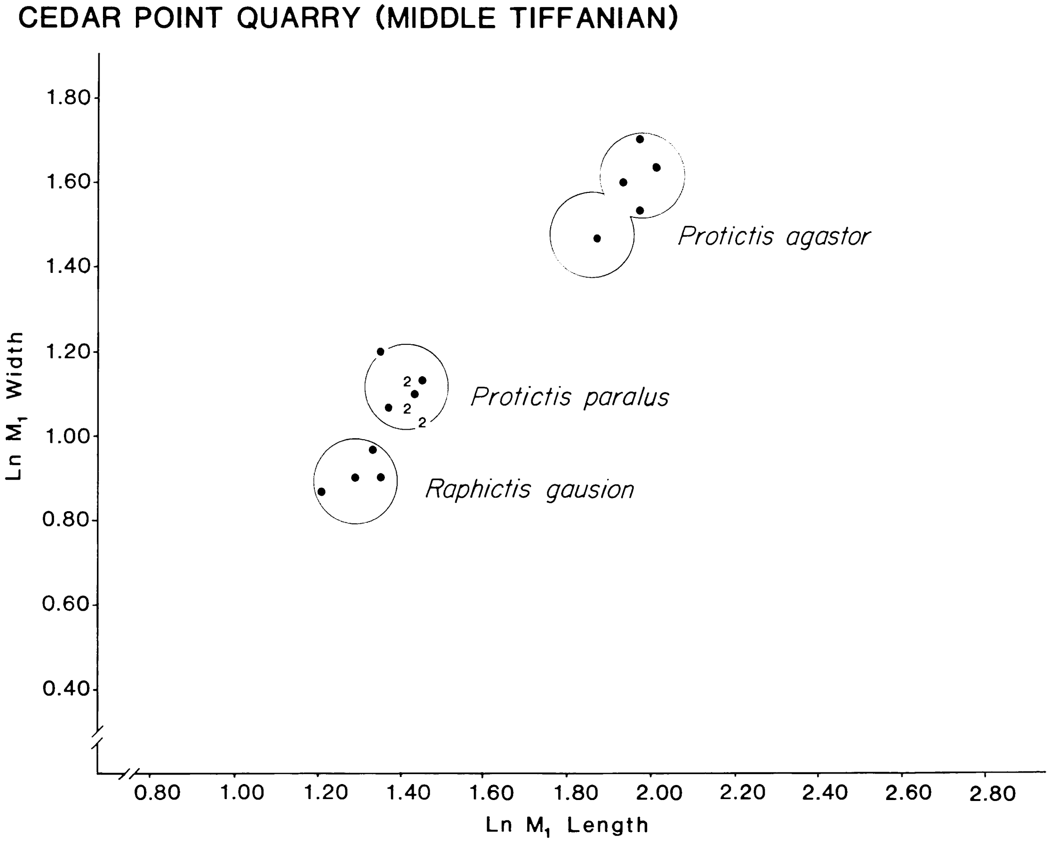


FIG. 3— Bivariate scatter of natural logarithm of crown length and natural logarithm of crown width (anterior width) of viverravid first lower molars from Cedar Point Quarry, middle Tiffanian (late Paleocene), in the northern Bighorn Basin, Wyoming. Abscissa and ordinate are the same as those in Figure 2. At least three species are represented. The observed range of variation in *Raphictis gausion* and in *Protictis paralus* is within 0.20 units on both the abscissa and ordinate. As interpreted here, *Protictis agastor* is sexually dimorphic, with females and males each having a range of variation approaching 0.20 units. Specimens included in *P. agastor* may, in fact, represent two distinct species but evidence at hand is insufficient to demonstrate this.

In the remainder of this section, previously described genera are discussed in order of their first appearance in the fossil record and increasing body size (*Simpsonictis*, *Ictidopappus*, *Bryanictis*, then *Protictis*), followed by a description of two new genera (*Intyrictis* and *Raphictis*). Within each genus, individual species and closely related species lineages are also discussed in order of stratigraphic appearance.

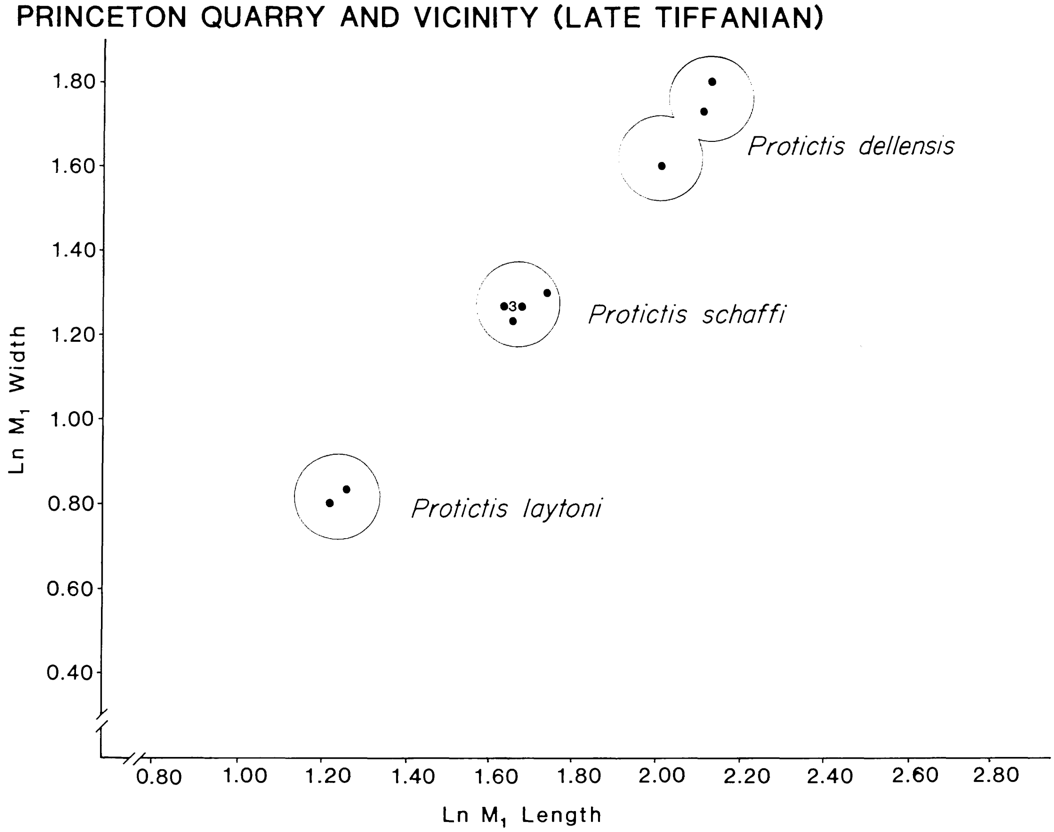


FIG. 4— Bivariate scatter of natural logarithm of crown length and natural logarithm of crown width (anterior width) of viverravid first lower molars from Princeton Quarry, late Tiffanian (late Paleocene), in the Clark's Fork Basin, Wyoming. Abscissa and ordinate are the same as those in Figures 2 and 3. A minimum of three species are represented. The observed range of variation in *Protictis laytoni* and in *Protictis schaffi* is within 0.20 units on both the abscissa and ordinate. As interpreted here, *Protictis dellensis* is sexually dimorphic, with females and males each having a range of variation approaching 0.20 units. Specimens included in *P. dellensis* may, in fact, represent two distinct species but evidence at hand is insufficient to demonstrate this.

Order CARNIVORA Bowdich, 1821
Family VIVERRAVIDAE Wortman and Matthew, 1899

Type genus.—*Viverravus* Marsh, 1872.

Included genera.—North America: *Simpsonictis* MacIntyre, 1962 [Torrejonian]; *Ictidopappus* Simpson, 1935 [Torrejonian]; *Bryanictis* MacIntyre, 1966 [Torrejonian]; *Intyrictis* new genus [Torrejonian]; *Protictis* Matthew, 1937 [Torrejonian and Tiffanian]; *Raphictis* new genus [Tiffanian]; *Viverravus* Marsh, 1872 [Clarkforkian-Uintan?]; *Didymictis* Cope, 1875 [Clarkforkian-Bridgerian], and, questionably, *Protictoides* Flynn and Galiano, 1982 [Uintan]. Asia: *Pappictidops* Qiu and Li, 1977 [late Paleocene and possibly earliest Eocene]. Europe: Cf. *Viverravus*, Rich, 1971 [early Eocene].

Age and distribution.—Early Paleocene through middle Eocene in western North America, late Paleocene and possibly earliest Eocene in Asia, and early Eocene of Europe.

Discussion.—Viverravidae and Miacidae differ from most other archaic carnivorous mammals in retaining a single pair of enlarged carnassial teeth, (P^4/M_1). Viverravidae differ from Miacidae principally in lacking M^3/M_3 while retaining a functional (and often moderately large) M^2/M_2. The Paleocene Viverravidae of North America are basically very similar to each other, as one would expect of early members of an adaptive radiation. *Protictis* is the most generalized form, although not necessarily the most primitive. Anticipating the diagnoses given below, *Protictis* has a P_4 of moderate width with a small anterior paraconid, large sectorial protoconid with no accessory metaconid, a small hypoconid, with a very slightly basined talonid. M_1 is simple and symmetrical in structure, with a high trigonid. The paraconid is large, approaching the size of the metaconid, and these two cusps make an acute angle with the protoconid. A basined talonid of moderate width is aligned with the major axis of the dentary behind the trigonid. M_2 is also simple and symmetrical, with a low trigonid and a narrow basined talonid. Upper molars of *Protictis* are much broader than they are long, sectorial, with reduced metacones, little trace of a metaconule.

Simpsonictis differs from *Protictis* in having a reduced paraconid on M_1, and in having a much higher trigonid on M_2. *Ictidopappus* differs from *Protictis* in having simple reduced premolars, and M_1 with a very open trigonid. *Bryanictis* differs from *Protictis* in having lower crowns on P_4 and M_1, and broader, more basined talonids on P_4 and M_{1-2}. Upper molars of *Bryanictis* are relatively large and rectangular, retaining a strong metacone and a distinct metaconule. *Intyrictis* resembles *Bryanictis* in having a relatively low trigonid on M_1, but *Intyrictis* differs from all other viverravids in having a distinct metaconid and broad basined talonid on P_4. *Raphictis* differs from *Protictis* in having a straight narrow P_4 lacking a basined talonid, and in having a twisted asymmetrical talonid on M_1 curving laterally away from the midline of the dentary. *Viverravus* is distinctive in having unreduced premolars, an open trigonid on M_1, and a broadly basined sectorial M_2. *Didymictis* has a low closed trigonid with a broad basined talonid on M_1, and a broadly basined crushing M_2.

Flynn and Galiano (1982) recently named *Protictoides* as a new Uintan (middle Eocene) subgenus of *Protictis*, based on an isolated upper premolar and an isolated lower premolar. While these specimens may be correctly identified as viverravid, they are certainly not adequate to substantiate a range extension of *Protictis* from the late Paleocene to the middle Eocene, nor are they adequate material on which to base a new genus. Any meaningful consideration of *Protictoides* must await discovery of more complete specimens.

The type species of Asian *Pappictidops*, *P. orientalis* Qiu and Li (1977), is unusual in having very reduced upper and lower second molars, and it is unusual in having the talonid on M_1 open medially. However, an older species, probably late Paleocene in age, *P. acies* (Wang, 1978), is much more similar to North American *Protictis* and its allies, and there can be little doubt that it belongs in Viverravidae.

We follow Van Valen (1967) in excluding *Quercygale* Kretzoi (= *Humbertia* de Beaumont) from Viverravidae. Hunt (1974) and Flynn and Galiano (1982) allied *Palaeogale* von Meyer, from the Oligocene of Europe, Asia, and North America, with *Viverravus* and Viverravidae. We follow Simpson (1946) and de Bonis (1981) in regarding *Palaeogale* as a primitive and divergently specialized mustelid.

Simpsonictis MacIntyre, 1962

Didymictis (in part), Simpson, 1935, p. 238; 1937, p. 212.
Simpsonictis MacIntyre, 1962, p. 3.
Protictis (*Simpsonictis*), MacIntyre, 1966, p. 168.

Type species.—Didymictis tenuis Simpson, 1935.

Included species.—Simpsonictis tenuis (Simpson)[Torrejonian], questionably *S. jaynanneae* Rigby [Torrejonian], and *S. pegus*, new species [Torrejonian].

Diagnosis.—Differs from all other Viverravidae in having a more triangular P_4 that is narrow at the front and broader at the back when viewed in occlusal outline, in having a more reduced paraconid on M_1, and in having a moderate to large M_2 with an unusually high trigonid.

Age and distribution.—Torrejonian Land-Mammal Age (middle Paleocene) of western North America. All of the known specimens come from localities in Montana and Wyoming. Gazin (1956, p. 35) and MacIntyre (1966, p. 173) reported specimens similar to *Simpsonictis tenuis* from Saddle Locality in the Bison Basin, Wyoming. If correctly allocated, these specimens extend the temporal range of *Simpsonictis* into the Tiffanian Land-Mammal Age (late Paleocene).

Discussion.—Simpsonictis, originally proposed as a distinct genus (MacIntyre, 1962), was later included as a subgenus of *Protictis* (MacIntyre, 1966). *Simpsonictis* is undoubtedly closely related to *Protictis*, but we recognize *Simpsonictis* as a full genus, in part because we interpret its distinctiveness as justifying this rank, and in part because we see little practical utility in attempting to express evolutionary relationships parenthetically.

Rigby (1980) named a new species, *Simpsonictis jaynanneae*, based on a single P^4 (holotype) and other isolated teeth from Swain Quarry (Torrejonian) in southwestern Wyoming. P^4 is not known in any specimen from Gidley Quarry or Rock Bench Quarry, and Rigby provides no measurements of his holotype. Consequently, it is difficult to compare *S. jaynanneae* with other specimens of *Simpsonictis*. Judging from statistics given by Rigby (1980, table 28), the Swain Quarry sample is only slightly larger than *Simpsonictis tenuis* and we suspect that it probably belongs to this species. It is much smaller than *Simpsonictis pegus* described here.

Simpsonictis tenuis (Simpson, 1935)
Fig. 5A-B

Didymictis tenuis Simpson, 1935, p. 238; 1937, p. 212, fig. 58.
Simpsonictis tenuis, MacIntyre, 1962, p. 4, fig. 1-3.
Protictis (*Simpsonictis*) *tenuis*, MacIntyre, 1966, p. 168, fig. 18, Pl. 12, fig. 1-8, Pl. 17, figs. 2,4,7.
Protictis cf. *tenuis*, Rose, 1981, p. 146, 149.

Holotype.—USNM 9297, left dentary with ?P_4 and M_1.

Type locality.—Gidley Quarry, Lebo Member of Fort Union Formation, Crazy Mountain Basin, Montana.

Age and distribution.—Torrejonian Land-Mammal Age (middle Paleocene). *S. tenuis* is known principally from Gidley Quarry in the Crazy Mountain Basin, Montana, and Rock Bench Quarry in the northern Bighorn Basin, Wyoming. It may be represented at Swain Quarry as well (Rigby, 1980, see discussion above).

Diagnosis.—Differs from *Simpsonictis pegus* in being significantly smaller in all comparable linear dimensions.

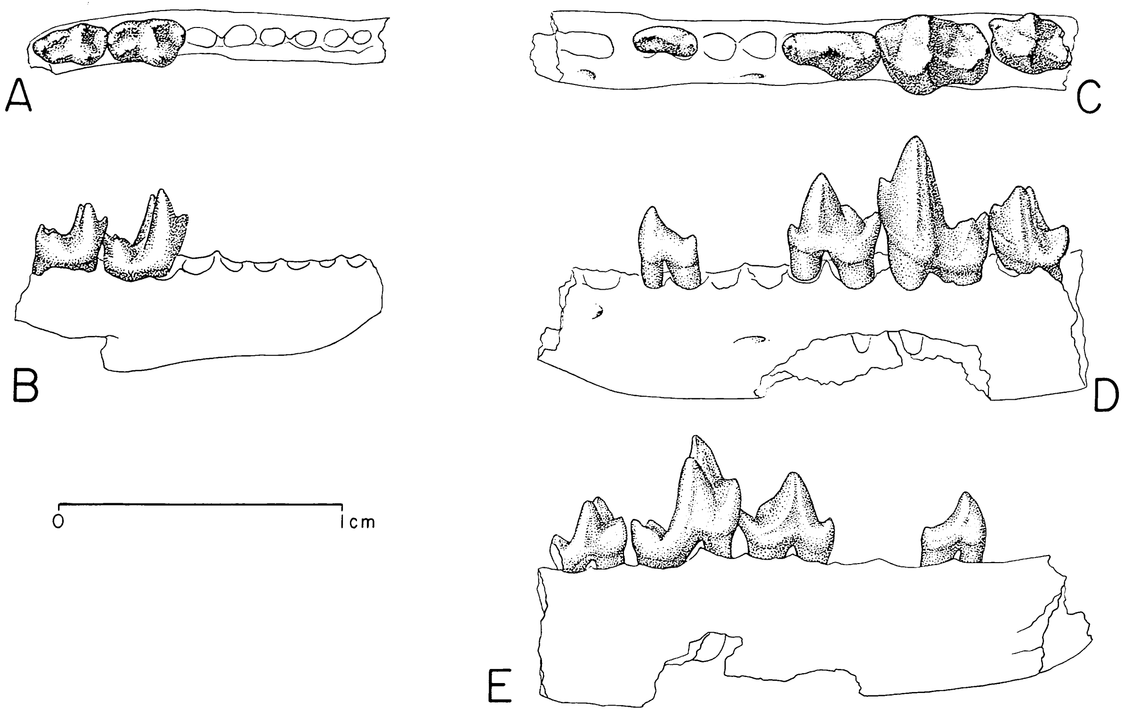


FIG. 5— Comparison of lower dentition of *Simpsonictis tenuis* and *Simpsonictis pegus* from Rock Bench Quarry (Torrejonian) in the northern Bighorn Basin, Wyoming. A-B, right dentary of *S. tenuis* with M_{1-2} (PU 17509) in occlusal (A) and lateral (B) view. C-E, left dentary of *S. pegus* with P_2 and P_4-M_2 (PU 17635) in occlusal (C), lateral (D), and medial (E) view. Note reduced paraconid on M_1 and relatively high trigonid on M_2 characteristic of *Simpsonictis*.

Description.—This species is adequately described in MacIntyre (1966) and new specimens from Rock Bench Quarry add no information not already preserved in those from Gidley Quarry. Measurements of the Rock Bench Quarry sample of this species are summarized in Table 1.

Typodigm.—AMNH 35347-35350 and USNM 9297 (holotype) from Gidley Quarry (see MacIntyre, 1966, p. 168). The following new specimens, all from Rock Bench Quarry, are referred to *Simpsonictis tenuis*: PU 17509 (R dent. M_{1-2}), 17510 (R dent. P_2P_4-M_1), and 17590 (L dent. M_1 talonid and M_2).

Simpsonictis pegus n. sp.
Fig. 5C-E

Protictis sp. nov., Rose, 1981, p. 146.

Holotype.—PU 17511, left dentary with P_2 and P_4-M_2.

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

TABLE 1 — Summary of measurements of lower cheek teeth of Torrejonian *Simpsonictis tenuis* from Rock Bench Quarry, northern Bighorn Basin, Wyoming. Measurements are defined in Figure 1. *N* = sample size, *OR* = observed range, $\bar{x}$ = mean, *S* = standard deviation, and *V* = coefficient of variation. All measurements in mm.

Tooth position		N	OR	$\bar{x}$	S	V
Lower dentition						
P_2	L	1	1.6	-	-	-
	W	1	0.8	-	-	-
P_3	L	-	-	-	-	-
	W	-	-	-	-	-
P_4	L	1	2.7	-	-	-
	W	1	1.2	-	-	-
M_1	L	2	2.8	2.80	-	-
	AW	2	1.7 - 1.8	1.75	-	-
	PW	2	1.4 - 1.7	1.55	-	-
	TL	2	1.6	1.60	-	-
	TH	2	3.1 - 3.5	3.30	-	-
M_2	L	2	2.6	2.60	-	-
	AW	2	1.3 - 1.4	1.35	-	-
	PW	2	1.1 - 1.2	1.15	-	-
	TH	1	2.1	-	-	-
Mand. depth		3	3.0 - 3.5	3.33	0.29	8.6

Age and distribution.—Torrejonian Land-Mammal Age (middle Paleocene), type locality only.

Diagnosis.—Differs from *Simpsonictis tenuis* and *S. jaynanneae* in being significantly larger in all comparable linear dimensions. Further differs in having a relatively broader trigonid on M_1.

Etymology.—*pegos*, Greek, strong or solid, in reference to the greater size of this species by comparison with *Simpsonictis tenuis.*

Description.—The upper dentition of *Simpsonictis pegus* is not yet known. Six dentaries collectively preserve alveoli for a large C_1, small single-rooted P_1, and intact crowns of all of the lower cheek teeth from P_2-M_2. The mandibular symphysis is long, shallow, and unfused, as is typical of Viverravidae. Two mental foramina are present on the dentary, one located below the alveolus for P_1 and the other below P_3. P_2 is small and double-rooted, with a simple crown having a large narrow protoconid and a much smaller posterior basal cusp (hypoconulid, following MacIntyre) directly behind and well separated from the protoconid. P_3 is larger, but otherwise very similar to P_2. The crown of P_4 has a distinct anterior basal cusp (paraconid), a large pointed protoconid, and a distinct hypoconulid angled medially from the midline of the crown. The crown of P_4 is somewhat triangular in occlusal outline, with the posterior part being much wider at the base than the anterior part. A hypoconid cusp is variably present on P_4 immediately behind the protoconid (it is well developed in the holotype, see Fig. 5).

M_1 has a high trigonid, as in all primitive viverravids. The paraconid is anterior to the metaconid and consistently reduced in size by comparison to the metaconid. The talonid of M_1 is aligned with the long axis of the dentary. It is basined, but narrower than the trigonid, with a large hypoconid, and smaller hypoconulid and entoconid cusps. M_2 is very similar to M_1, but smaller. It too has a high trigonid with a reduced paraconid and a basined talonid of moderate width. The hypoconulid is a large posterior cusp on the talonid of M_2.

Measurements of the holotype of *Simpsonictis pegus* are as follows: $P_2L = 2.2$, $W = 1.0$; $P_4L = 3.6$, $W = 1.7$; $M_1L = 3.7$, $AW = 2.7$, $PW = 2.1$, $TL = 2.3$, $TH = 4.7$; $M_2AW = 1.9$, $TH = 2.8$. Measurements of the entire sample of this species are summarized in Table 2.

Typodigm.—PU 14232 (L dent. M_{1-2}), 17466 (L dent. P_4-M_1), 17511 (holotype, L dent. P_2 and P_4-M_2), 17575 (R dent. M_1), 17635 (R dent. $_{2-4}$), and 18682 (R dent. M_{1-2}), all from Rock Bench Quarry (Rose, 1981, p. 147).

TABLE 2 — Summary of measurements of lower cheek teeth of Torrejonian *Simpsonictis pegus* from Rock Bench Quarry, northern Bighorn Basin, Wyoming. Measurements are defined in Figure 1. Abbreviations as in Table 1.

Tooth position		N	OR	$\bar{X}$	S	V
Lower dentition						
P_2	L	2	2.1 - 2.2	2.15	-	-
	W	2	0.9 - 1.0	0.95	-	-
P_3	L	1	2.7	-	-	-
	W	1	1.2	-	-	-
P_4	L	3	3.6 - 3.8	3.70	0.10	2.7
	W	2	1.7	1.70	-	-
M_1	L	5	3.3 - 3.8	3.62	0.19	5.3
	AW	4	2.6 - 2.9	2.73	0.13	4.6
	PW	4	1.9 - 2.3	2.08	0.17	8.2
	TL	4	2.1 - 2.3	2.23	0.10	4.3
	TH	2	4.3 - 4.7	4.50	-	-
M_2	L	2	3.3 - 3.4	3.35	-	-
	AW	3	1.9 - 2.1	1.97	0.12	5.9
	PW	2	1.5 - 1.6	1.55	-	-
	TH	3	2.5 - 3.1	2.80	0.30	10.7
Mand. depth		3	4.8 - 6.1	5.40	0.66	12.1

Ictidopappus Simpson, 1935

Ictidopappus Simpson, 1935, p. 237; 1937, p. 213. MacIntyre, 1966, p. 140.

Type species.—*Ictidopappus mustelinus* Simpson, 1935.

Included species.—Type species only. MacIntyre (1966) referred a lower premolar of Puercan age to "?Cf. *Ictidopappus*, unnamed new species," but this premolar is so different from those of *Ictidopappus* that it is very unlikely to represent this genus.

Diagnosis.—Differs from all other Viverravidae in having reduced lower premolars with simple triangular crowns and in having a more open trigonid on M_1.

Age and distribution.—Torrejonian Land-Mammal Age (middle Paleocene) in western North America.

Ictidopappus mustelinus Simpson, 1935

Ictidopappus mustelinus Simpson, 1935, p. 237; 1937, p. 214, figs. 60-61. MacIntyre, 1966, p. 140, figs. 9-11, Pl. 1, figs. 1-4, Pl. 2, figs. 5-8.

Holotype.—USNM 9296, right dentary with $P_{3-4}M_{1-2}$.

Type locality.—Gidley Quarry, Lebo Member of Fort Union Formation, Crazy Mountain Basin, Montana.

Age and distribution.—Torrejonian Land-Mammal Age (middle Paleocene). This species is presently known only from the type locality.

Diagnosis.—As for the genus.

Description.—Known specimens of *Ictidopappus mustelinus* are adequately described in Simpson (1937, p. 214) and MacIntyre (1966, p. 140).

Typodigm.—USNM 9295 and 9296 (holotype) from Gidley Quarry (MacIntyre, 1966, p. 140). No additional specimens have been discovered at Gidley Quarry or Rock Bench Quarry.

Bryanictis MacIntyre, 1966

Didymictis (in part), Simpson, 1935, p. 238; 1937, p. 209.
Protictis (*Bryanictis*) MacIntyre, 1966, p. 176.

Type species.—*Didymictis microlestes* Simpson, 1935.

Included species.—Type species only.

Diagnosis.—Differs from all other viverravids in having a more prominent lingual cingulum on M^1 and in combining a short trigonid with a prominent paraconid, low protoconid, and broad talonid on M_1. M_2 has a short trigonid of moderate height, and a broad basined talonid. Differs from *Simpsonictis* and *Protictis* in having a relatively lower trigonid and a much broader talonid on M_1. Differs from *Ictidopappus* in having larger premolars and a shorter trigonid on M_1.

Age and distribution.—Torrejonian Land-Mammal Age (middle Paleocene).

Discussion.—MacIntyre (1966, p. 190) described a new species, *Protictis* (*Bryanictis*) *vanvaleni*, from the Torrejonian Nacimiento Formation of the San Juan Basin, New Mexico. The type (AMNH 16031) and referred specimens are fragmentary but unlike any other viverravid known. According to MacIntyre, *P.* (*B.*) *vanvaleni* is similar in size to *B. microlestes*, but this is not sufficient to warrant inclusion in *Bryanictis*. We here remove "*Bryanictis*" *vanvaleni* from *Bryanictis* and place it in a new genus *Intyrictis* (see below).

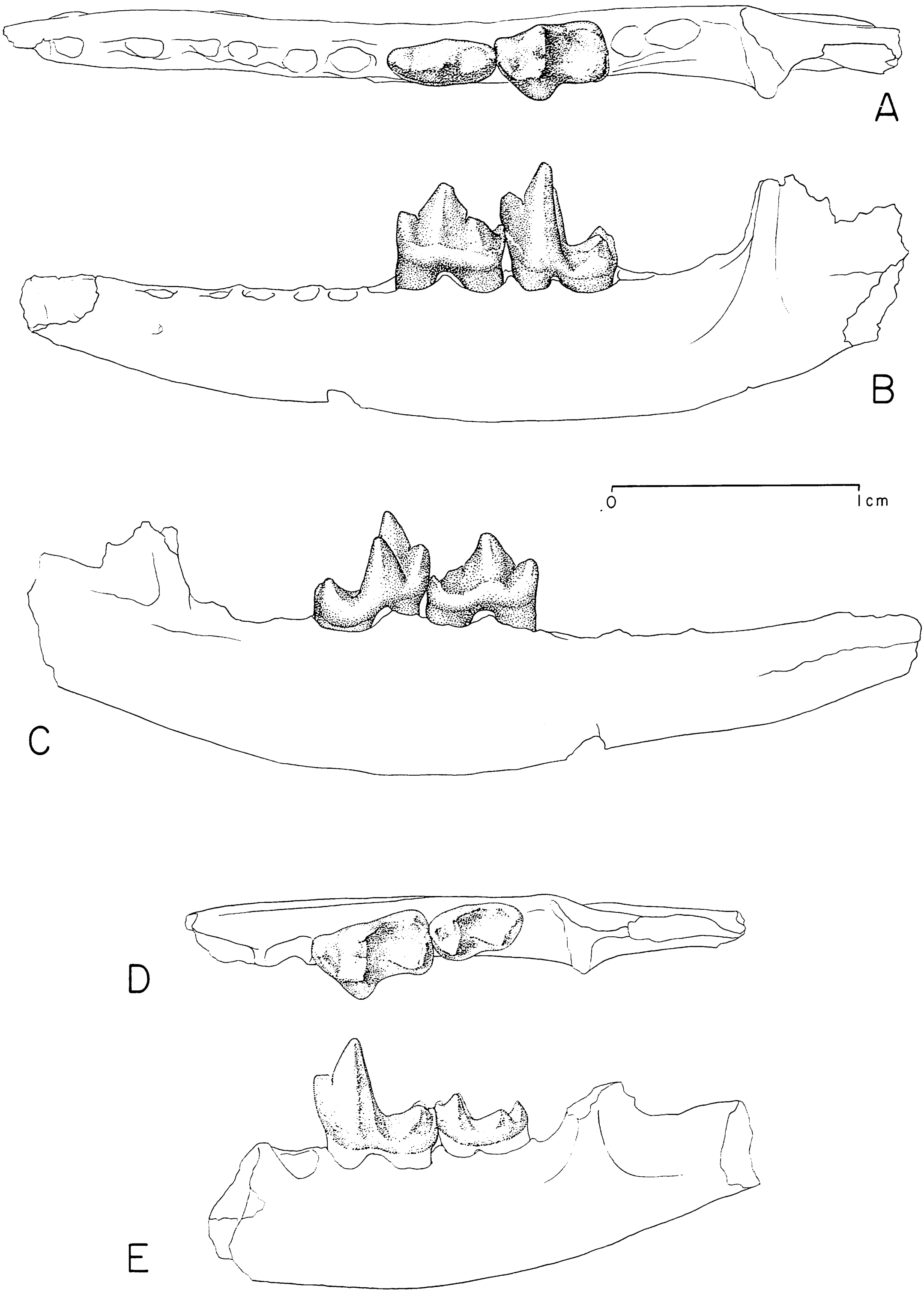
Bryanictis microlestes (Simpson, 1935)
Fig. 6, 8A-B

Didymictis microlestes Simpson, 1935, p. 238; 1937, p. 210, fig. 56-57.
Protictis (*Bryanictis*) *microlestes*, MacIntyre, 1966, p. 177, fig. 19, Pl. 13, figs. 1-4, Pl. 14, figs. 1-4, Pl. 15, figs. 1-8, Pl. 16, figs. 1-5, 7, Pl. 17, figs. 1, 3, 6, 9, Pl. 18, figs. 2-5.
Protictis microlestes, Rose, 1981, p. 146, 149.

Holotype.—USNM 9301, left dentary with P_4-M_2.

Type locality.—Gidley Quarry, Lebo Member of Fort Union Formation, Crazy Mountain Basin, Montana.

FIG. 6— Lower dentition of *Bryanictis microlestes* from Rock Bench Quarry (Torrejonian) in the northern Bighorn Basin, Wyoming. A-C, left dentary with P_4-M_1 (PU 14253) in occlusal (A), lateral (B), and medial (C) view. D-E, left dentary with M_{1-2} (PU 14254) in occlusal (D) and lateral (E) view. Note low trigonid on M_1 and anteroposteriorly short trigonid on M_2 characteristic of *Bryanictis*. Trigonid is narrower than talonid on some specimens.


A
B
0
1 cm
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D
E

Age and distribution.—Torrejonian Land-Mammal Age (middle Paleocene). *B. microlestes* is known principally from Gidley Quarry in the Crazy Mountain Basin, Montana (type locality), and from Rock Bench Quarry in the northern Bighorn Basin, Wyoming.

Diagnosis.—As for the genus.

Description.—*Bryanictis microlestes* is adequately described by Simpson (1937) and MacIntyre (1966), and new specimens from Rock Bench Quarry do not add any information not already evident in those from Gidley Quarry. Measurements of the Rock Bench Quarry sample are summarized in Table 3.

TABLE 3 — Summary of measurements of upper and lower cheek teeth of Torrejonian *Bryanictis microlestes* from Rock Bench Quarry, northern Bighorn Basin, Wyoming. Measurements are defined in Figure 1. Abbreviations as in Table 1.

Tooth position		N	OR	$\bar{x}$	S	V
Upper dentition						
M^1	L	1	4.6	-	-	-
	AW	1	5.2	-	-	-
	PW	1	4.6	-	-	-
	TL	1	3.0	-	-	-
Lower dentition						
P_2	L	1	2.4	-	-	-
	W	1	1.1	-	-	-
P_3	L	1	3.9	-	-	-
	W	2	1.6 - 1.7	-	-	-
P_4	L	4	4.1 - 4.7	4.48	0.26	5.9
	W	5	1.9 - 2.2	2.06	0.11	5.5
M_1	L	11	4.4 - 4.8	4.66	0.13	2.8
	AW	11	2.8 - 3.1	2.99	0.10	3.5
	PW	11	2.5 - 3.1	2.76	0.16	5.7
	TL	11	2.3 - 2.6	2.54	0.10	4.1
	TH	6	4.4 - 4.7	4.58	0.12	2.6
M_2	L	4	3.9 - 4.0	3.95	0.06	1.5
	AW	4	2.3 - 2.6	2.43	0.15	6.2
	PW	4	2.1 - 2.2	2.13	0.05	2.4
	TH	4	2.2 - 2.4	2.33	0.10	4.1
Mand. depth		8	5.1 - 6.4	5.66	0.42	7.5

Typodigm.—AMNH 35360-35388 and USNM 8631, 9298-9300, 9301 (holotype), 9302-9308, 9310, 9581, 9855, 10049 are known from Gidley Quarry. USNM 6146, 6147, 9875, 12151, and 16870 are known from Silberling Quarry and other localities in the Crazy Mountain Basin (MacIntyre, 1966, p. 177). New specimens from Rock Bench Quarry referred to *Bryanictis microlestes* include: PU 14253 (L dent. P_4-M_1), 14254 (L dent. M_{1-2}), 14255 (R dent. P_{3-4}), 17723 (L dent. P_4-M_1), 17724 (R dent. P_4-M_1), 17725 (L dent. M_{1-2}), 17726 (L dent. M_{1-2}), 17727 (L dent. P_{2-3}), 18528 (R iso. M_1), 18529 (L iso. M^1), 18687 (R dent. M_2), 19053 (L dent. P_4-M_1), 20616 (L dent. M_1), and several isolated lower molars (unnumbered) including two R iso. M_1s.

Protictis Matthew, 1937

Didymictis (in part). Cope. 1882, p. 464; 1884, p. 306. Matthew. 1897, p. 287. Simpson. 1935, p. 238; 1937, p. 209. Dorr. 1952, p. 85.
Viverravus (in part). Matthew. 1899, p. 29. Wortman. 1901, p. 145.
Didymictis (*Protictis*) Matthew, 1937, p. 101.
Protictis (in part). MacIntyre, 1966, p. 148.
Protictis (*Protictis*). MacIntyre, 1966, p. 149. Holtzman. 1978, p. 52.

Type species.—Protictis haydenianus Cope, 1882.

Included species.—Protictis haydenianus (Cope) [Torrejonian], *P. paralus* Holtzman [middle Tiffanian], *P. agastor* n. sp. [middle-late Tiffanian], *P. laytoni* n. sp. [late Tiffanian], *P. schaffi* n. sp. [late Tiffanian], and *P. dellensis* (Dorr) [late Tiffanian].

Diagnosis.—Generalized viverravid with moderately wide P_4, having a sectorial protoconid, small hypoconid, and a very slightly basined talonid. M_1 simple and symmetrical with high trigonid, prominent paraconid nearly equal in size to metaconid. Paraconid, protoconid, and metaconid form acute angle. Talonid basined, narrower than trigonid, and aligned anteroposteriorly with dentary. M_2 simple and symmetrical, with low trigonid and narrow basined talonid. Upper molars much broader than long, with reduced metaconid and little or no trace of metaconule or lingual cingulum.

Age and distribution.—Protictis is known from Torrejonian and Tiffanian (middle-late Paleocene) age faunas in western North America, ranging from New Mexico to Montana.

Discussion.—As noted above, *Protictis* (*Protictoides*) described by Flynn and Galiano (1982) from the Uintan (middle Eocene) of western Wyoming, is based on such fragmentary material that it cannot be allocated reliably to any known genus of Viverravidae. Consequently, this new record is inadequate evidence that *Protictis* survived through the middle Eocene.

Protictis haydenianus (Cope, 1882)
Fig. 7

Didymictis haydenianus Cope, 1882, p. 464; 1884, p. 306, Pl. 23e, figs. 12-13. Matthew, 1897, p. 287; 1909, p. 361. Simpson, 1937, p. 213, fig. 59.
Didymictis primus Cope, 1884, p. 309.
Viverravus haydenianus, Matthew, 1899, p. 29. Wortman, 1901, p. 145.
Didymictis (*Protictis*) *haydenianus*, Matthew, 1937, p. 102, Pl. 15, figs. 3-5, Pl. 16, figs 2-3.
Protictis (*Protictis*) *haydenianus*, MacIntyre, 1966, p. 149, figs. 13-17, Pl. 3, figs. 1-11, Pl. 4, figs. 1-9, Pl. 5, figs. 1-6, Pl. 6, figs. 1-6, Pl. 7, figs. 1-4, Pl. 8, figs. 2, 3, 5, 8, 10, Pl. 9, figs. 1-11, Pl. 11, figs. 1-4, Pl. 20, figs. 1-2.
Protictis haydenianus, Rose, 1981, p. 146, 149.

Holotype.—AMNH 3368, left dentary with P_4-M_2, left maxilla with P^3-M^2.

Type locality.—San Juan Basin, New Mexico. MacIntyre (1966, p. 132, 166) indicates that the holotype probably came from the lower level (*Deltatherium* zone or biochron) of the Torrejonian near Chico Spring at the head of Gallegos Canyon (AMNH locality no. 1).

Age and distribution.—Torrejonian Land-Mammal Age (middle Paleocene) of western North America. This species ranges from New Mexico to Montana.

Diagnosis.—Differs from *Protictis paralus*, *P. laytoni*, and *P. schaffi* in being significantly larger. Differs from *P. agastor* and *P. dellensis* in having a more sectorial M_2, with a shorter, less massive trigonid. Further differs from *P. dellensis* in being significantly smaller.

FIG. 7— Lower dentition of *Protictis haydenianus* from Rock Bench Quarry (Torrejonian), northern Bighorn Basin, Wyoming. Right dentary with M_{1-2} (PU 16602) in occlusal (A), lateral (B), and medial (C) view. Note high trigonid with paraconid similar in size to metaconid and moderate symmetrical talonid on M_1 characteristic of *Protictis*. Note also small, narrow, somewhat sectorial crown of M_2 characteristic of *Protictis haydenianus*.

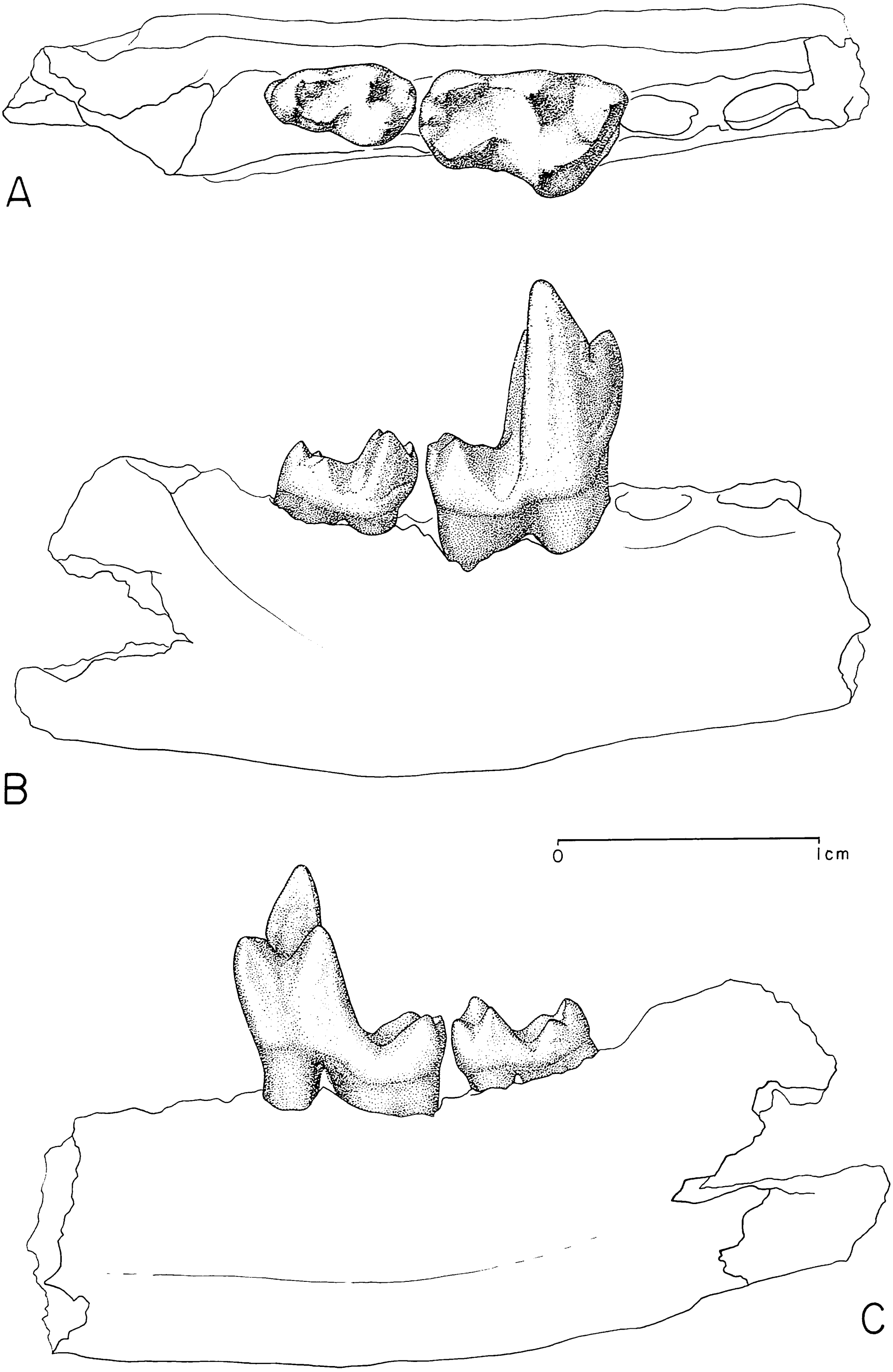
A
B
0
1cm
C

TABLE 4 — Summary of measurements of upper and lower cheek teeth of Torrejonian *Protictis haydenianus* from Rock Bench Quarry, northern Bighorn Basin, Wyoming. Measurements are defined in Figure 1. Abbreviations as in Table 1.

Tooth position		N	OR	$\bar{X}$	S	V
Upper dentition						
P^4	L	1	8.0	-	-	-
	W	1	6.1	-	-	-
M^1	L	1	5.8	-	-	-
	AW	1	8.4	-	-	-
	PW	1	7.6	-	-	-
	TL	1	4.0	-	-	-
Lower dentition						
P_4	L	-	-	-	-	-
	W	1	2.8	-	-	-
M_1	L	5	6.4 - 7.5	6.96	0.44	6.4
	AW	5	4.3 - 5.0	4.74	0.30	6.3
	PW	5	3.4 - 3.8	3.66	0.17	4.6
	TL	5	3.7 - 4.4	4.16	0.29	6.9
	TH	4	7.2 - 8.7	8.15	0.66	8.1
M_2	L	5	4.5 - 5.3	5.00	0.33	6.6
	AW	4	2.8 - 3.4	3.18	0.26	8.3
	PW	5	2.1 - 2.7	2.42	0.22	9.0
	TH	4	2.8 - 3.5	3.30	0.34	10.2
Mand. depth		2	8.3 - 9.5	8.90	-	-

Description.—*Protictis haydenianus* is adequately described and illustrated by Cope (1884), Matthew (1937), and MacIntyre (1966). New specimens from Rock Bench Quarry duplicate those known previously from the San Juan Basin, New Mexico, and Gidley Quarry, Montana. Measurements of the Rock Bench sample of *Protictis haydenianus* are summarized in Table 4.

Discussion.—*Protictis haydenianus* is older than all of the other known species of *Protictis*, and it is sufficiently generalized morphologically to be a plausible common ancestor of *P. paralus*, *P. laytoni*, and *P. schaffi*, on one hand, with sectorial second molars, and *P. agastor* and *P. dellensis*, on the other hand, with more massive second molars.

Typodigm.—AMNH 3368 (holotype) is the only specimen known to come from the type locality, although AMNH 1776, 3244a, 3369a, 3372, 3374, 3453a, 3517, 3996c, 4005, and 4060 may come from this locality as well (MacIntyre, 1966, p. 150). MacIntyre lists AMNH 948, 1764, 16539, 16540, 17059, and USNM 15345, 15346 as probably coming from early Torrejonian age strata in the San Juan Basin; AMNH 778, 1499, 1765, 2391, 2393, 15991-15995, 16536-16538, and USNM 5872, 15347-15354 as probably coming from late Torrejonian age strata in the San Juan Basin; and AMNH 3371 (type of synonym *Didymictis primus*), 12382 as coming from unknown Torrejonian levels in the San Juan Basin. In the Crazy Mountain Basin, Gidley Quarry yielded AMNH 35389-35392, 35862, and Silberling Quarry yielded USNM 6145 (MacIntyre, 1966, p. 150).

New specimens from Rock Bench Quarry referred to *Protictis haydenianus* include: PU 14090 (L dent. M_{1-2}), 16602 (R dent. M_{1-2}), 16603 (L dent. P_4-M_2), 18516 (R dent. M_2), 18517 (R iso. M_2), 18518 (L iso. M_1), 18519 (R iso. M^1), 18520 (R iso. M_1), and 18522 (R iso. P^4).

Protictis paralus Holtzman, 1978

Fig. 8C-F

Protictis (*Protictis*) *paralus* Holtzman, 1978, p. 52, Pl. 10, figs. 1-3.
Protictis cf. *paralus*, Rose, 1981, p. 152.

Holotype.—SMM P77.6.64, right dentary with C_1P_4-M_2.

Type locality.—Judson locality, Tongue River Member of Fort Union Formation, Williston Basin, North Dakota.

Age and distribution.—Middle Tiffanian Land-Mammal Age (late Paleocene). This species is presently known from the northern Bighorn Basin, Wyoming, and Williston Basin of western North Dakota.

Diagnosis.—Differs from *Protictis laytoni* in being significantly larger. Differs from *Protictis schaffi*, *P. agastor*, and *P. dellensis* in being significantly smaller. Further differs from *P. agastor* and *P. dellensis* in having a more sectorial M_2, with a shorter, less massive trigonid.

Description.—Cedar Point specimens of this species are fragmentary. None is as complete as the holotype, and none adds any information not readily apparent in the type sample from Judson. The isolated M^1 from Judson described by Holtzman (1978; SMM P77.7.139) is similar in proportion to M^1 in later *Protictis schaffi* (described here), and it lacks any trace of a lingual cingulum.

The lower dentition of *P. paralus* is also very similar in comparable parts to that of *P. schaffi*, differing principally in being significantly smaller in all dimensions. The holotype dentary of *P. paralus* has four mental foramina, one beneath each of the premolars. However, the two most complete dentaries of this species from Cedar Point Quarry have only two mental foramina, beneath P_1 and P_3 (as in *P. schaffi* and most viverravids).

Measurements of the holotype of *Protictis paralus* are as follows: $C_1L = 2.1$, $W = 1.4$; $P_4L = 4.1$, $W = 1.8$; $M_1L = 4.1$, $AW = 2.9$, $PW = 2.3$, $TL = 2.6$, $TH = 4.5$; $M_2L = 3.6$, $AW = 2.0$, $PW = 1.8$, $TH = 2.5$ (est.); and mandibular depth beneath $M_1 = 5.6$. Measurements of the Cedar Point Quarry sample of *Protictis paralus* are summarized in Table 5.

Discussion.—Middle Tiffanian *Protictis paralus* resembles later *P. laytoni* and *P. schaffi* in having a sectorial rather than massive M_2. It is intermediate in size, and a plausible common ancestor of both later species.

Typodigm.—SMM P77.6.64 (holotype) and P77.7.139 from Judson (Holtzman, 1978). New specimens from Cedar Point Quarry include: PU 20056 (L dent. M_1), 20647 (L dent. M_1), 21362 (L dent. P_4-M_1), 21428 (R dent. M_2), 21851 (R dent. M_1), 22011 in part (numerous isolated teeth, including complete crowns of three iso. M_1s), 22012 (R iso. M_1), 22013 (R dent. P_4-M_1), 22014 (R dent. P_4-M_1), UM 64575 (L dent. M_1), 64576 (L dent. P_4), and 64639 in part (R iso. M_1, L iso. M_1, L iso. P_4).

Protictis laytoni n. sp.

Fig. 9

Viverravine sp. A, Rose, 1981, p. 156.

Holotype.—PU 16523, right dentary with alveoli for all premolars, an intact crown of M_1, and alveoli for M_2.

Type locality.—Princeton Quarry, Fort Union Formation, Clark's Fork Basin, Wyoming.

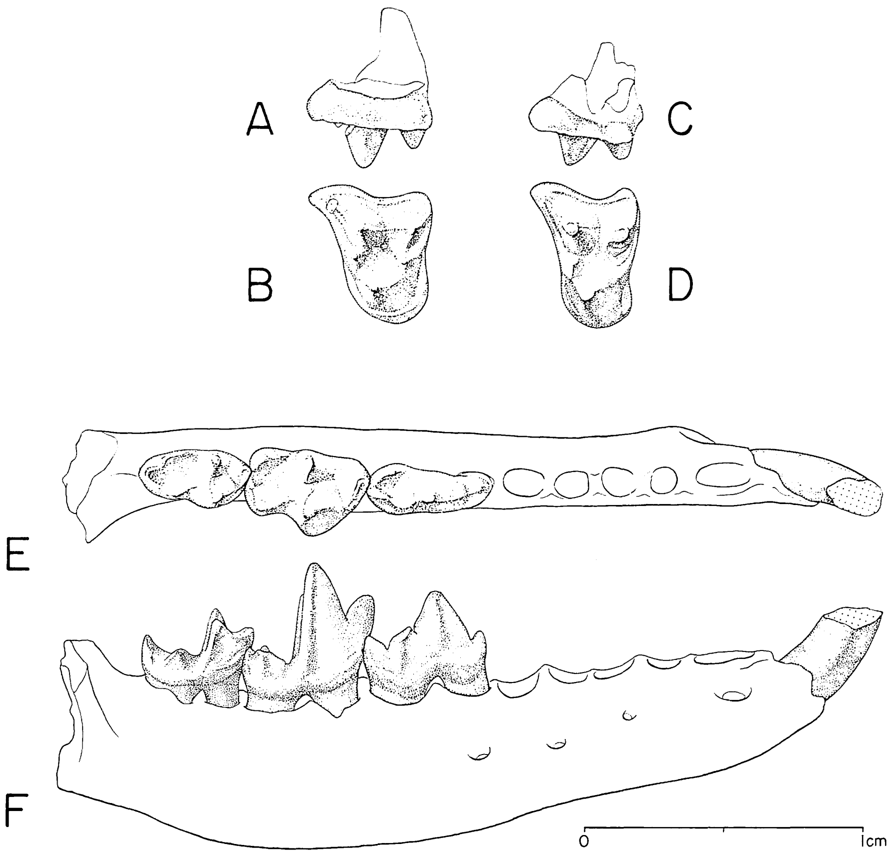

FIG. 8 — Dentition of *Bryanictis microlestes* from Rock Bench Quarry (Torrejonian) in the northern Bighorn Basin, and *Protictis paralus* from Judson (middle Tiffanian) in the Williston Basin, North Dakota. A-B, Left M^1 of *Bryanictis microlestes* (PU 18529) in lateral and occlusal view. C-D, Left M^1 of *Protictis paralus* (SMM P77.7.139) in lateral and occlusal view. E-F, Right dentary of *Protictis paralus* with C_1 and P_4-M_2 (holotype, SMM P77.6.64) in occlusal and lateral view. Note strong lingual cingulum on M^1 characteristic of *Bryanictis*, and reduced lingual cingulum on M^1 of *Protictis*. Note also sectorial crown of M_2 characteristic of *Protictis paralus* and *P. schaffi*.

Age and distribution.—Late Tiffanian Land-Mammal Age (late Paleocene). This species is known only from the type locality in northwestern Wyoming.

Diagnosis.—Smallest species of *Protictis*. Differs from all other species in being markedly smaller, and in having a more delicate M_1 with a more gracile crown and less massive trigonid cusps.

Etymology.—Named for Mr. Robert Layton, who found the type specimen while collecting for Princeton University in 1936.

Description.—The holotype dentary preserves part of a shallow, unfused mandibular symphysis. There are mental foramina beneath P_1 and P_3 on the labial side of the jaw. Part of the canine alveolus is preserved, as are alveoli for P_{1-4}, an intact crown of M_1, and alveoli for M_2. Judging from alveoli, P_1 had two roots fused together and the remaining premolars were double-rooted. The crowns of M_1 in PU 16523 (holotype) and 17844 are virtually identical in form. Both have a broad trigonid with a high protoconid and lower paraconid and metaconid cusps. The

TABLE 5 — Summary of measurements of lower cheek teeth of middle Tiffanian *Protictis paralus* from Cedar Point Quarry, northern Bighorn Basin, Wyoming. Measurements are defined in Figure 1. Abbreviations as in Table 1.

Tooth position		N	OR	$\bar{x}$	S	V
Lower dentition						
P_4	L	5	3.7 - 4.2	4.02	0.19	4.8
	W	5	1.7 - 2.0	1.86	0.11	6.1
M_1	L	10	3.9 - 4.3	4.14	0.13	3.3
	AW	17	2.8 - 3.8	3.05	0.24	7.7
	PW	10	2.0 - 2.4	2.21	0.11	5.0
	TL	17	2.5 - 2.9	2.66	0.12	4.4
	TH	15	4.9 - 5.5	5.08	0.18	3.5
M_2	L	1	4.4	-	-	-
	AW	1	2.4	-	-	-
	PW	1	2.2	-	-	-
	TH	-	-	-	-	-
Mand. depth		6	5.5 - 6.7	6.03	0.39	6.4

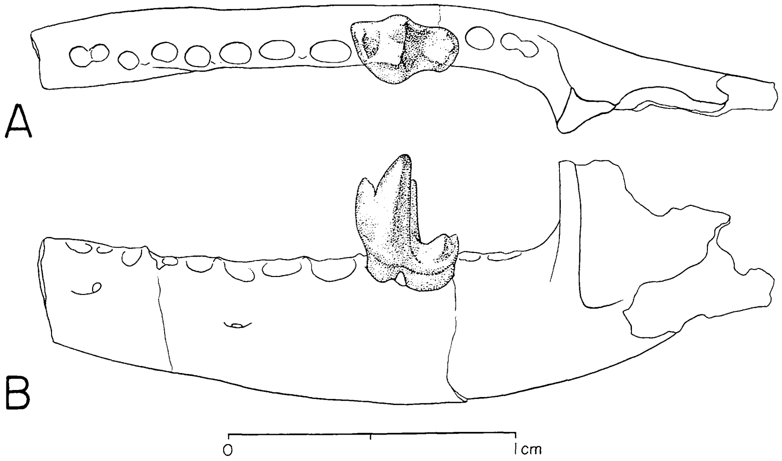

FIG. 9— Lower dentition of *Protictis laytoni* from Princeton Quarry (late Tiffanian) in the Clark's Fork Basin, Wyoming. Left dentary with M_1 (holotype, PU 16523) in occlusal (A) and lateral (B) view.

paraconid and metaconid are approximately equal in height. The trigonid on M_1 is not as open as that of *P. schaffi*, and the trigonid cusps themselves appear to be less robust. The talonid of M_1 is moderate in width, with the hypoconid being the largest talonid cusp and the hypoconulid and entoconid being somewhat smaller.

The holotype is larger than the one additional referred specimen in all dimensions measured except talonid width. Measurements of both Princeton Quarry specimens of *Protictis laytoni* are listed in Table 6.

Typodigm.—PU 16523 (holotype, L dent. M_1), and 17844 (L iso. M_1), both from Princeton Quarry.

TABLE 6 — Summary of measurements of lower cheek teeth of late Tiffanian *Protictis laytoni* from Princeton Quarry, Clark's Fork Basin, Wyoming. Measurements are defined in Figure 1. Abbreviations as in Table 1.

Tooth position		N	OR	$\bar{x}$	S	V
Lower dentition						
M_1	L	2	3.4 - 3.5	3.45	-	-
	AW	2	2.2 - 2.3	2.25	-	-
	PW	2	1.6 - 1.7	1.65	-	-
	TL	2	2.0 - 2.1	2.05	-	-
	TH	2	3.7 - 4.1	3.90	-	-
Mand. depth		1	4.5	-	-	-

Protictis schaffi n. sp.

Fig. 10, 11

Cf. *Viverravus* sp. nov., Rose, 1981, p. 156.

Holotype.—PU 19365, associated left dentary with P_2-M_1 and right dentary with $C_1P_1P_3$-M_2.

Type locality.—Schaff Quarry, Fort Union Formation, Clark's Fork Basin, Wyoming.

Age and distribution.—Late Tiffanian Land-Mammal Age (late Paleocene). This species is known from several localities, all in the same restricted stratigraphic interval in the Clark's Fork Basin of northwestern Wyoming.

Diagnosis.—Differs from all other species of *Protictis* in having a slightly more open trigonid on M_1. Differs from *Protictis paralus* and *P. laytoni* in being significantly larger (ca. 29% or 55% larger, respectively, in linear dimensions). Differs from *P. agastor* and *P. dellensis* in being significantly smaller (ca. 24% or 34% smaller, respectively, in linear dimensions), and further differs from these species in having a more sectorial M_2 with a less massive trigonid.

Etymology.—Named for Mr. Charles Schaff, now of Harvard University, who discovered the type locality, and, indirectly, this specimen, while leading a Princeton field party.

Description.—*Protictis schaffi* is now one of the best known species of *Protictis*, being represented by a compressed but otherwise nearly complete cranium, six maxillae, and dentaries of eight different individuals from Princeton Quarry, Schaff Quarry, and other localities in the vicinity. The cranium, PU 16495, is illustrated in Figure 11. It is the first known of *Protictis* preserving the basicranium. The total condylobasal length of this specimen, as preserved, is 70 mm, and it is estimated to have been about 30-35 mm in maximum breadth across the zygomatic arches. The left premaxilla preserves alveoli for three small incisors that were approximately equal in size. The left maxilla preserves a large canine alveolus, followed by alveoli for three double-rooted premolars (P^{1-3}) and intact crowns of P^4-M^2. Broken P^4-M^2 are preserved on the right side of the palate. Hence the upper dental formula of *Protictis* was 3.1.4.2, and the lower formula was presumably the same (the number of lower incisors cannot be determined with certainty in any known specimen).

The crown of P^2 is preserved in PU 13964. It is very simple, with a large central cusp (paracone?) and a very small posterior cuspule at the base of the crown. A distinct oblique ridge runs forward and medially from the paracone to the base of the crown at its anterolingual margin. P^3 is larger than P^2, but identical to it in form. The oblique anterior ridge in both appears to be serially homologous with the postprotocristid on P^4 (such as it is) and following molars. The crown of P^4 is triangular in occlusal outline, with corners defined by a small anterior parastylar cusp, a lingually placed protocone, and a crestlike posterolabial metastyle. The largest

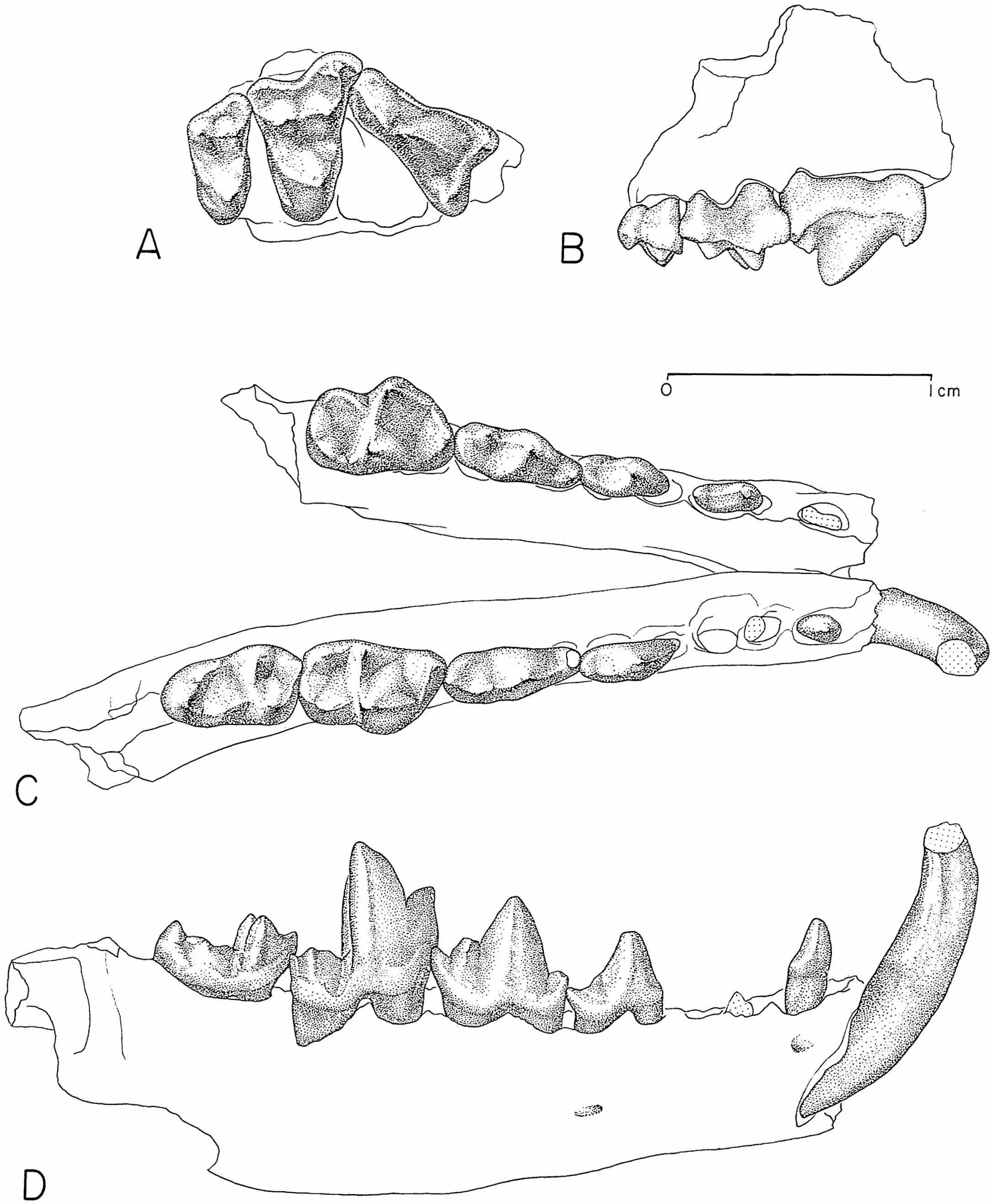

FIG. 10— Upper and lower dentition of *Protictis schaffi* from Princeton and Schaff quarries (late Tiffanian) in the Clark's Fork Basin, Wyoming. A-B, right maxilla with P^4-M^2 from Princeton Quarry (PU 14441) in occlusal (A) and lateral (B) view. C-D, left dentary with P_2-M_1 and right dentary with C_1-P_1 and P_3-M_2 from Schaff Quarry (holotype, PU 19365) in occlusal (C) and right lateral (D) view. Note partially open trigonid of M_1 characteristic of this species, and sectorial crown of M_2 characteristic of this species and *P. paralus*. The trigonid of M_1 in later *Viverravus* is even more open, with the paraconid placed more anteriorly.

cusp is a centrally positioned paracone, and the principal carnassial shearing crest is the postparacrista connecting the paracone and metastyle. There are no other accessory cusps on P^4.

The crown of M^1 is also basically triangular, with a large protocone, large paracone, and smaller metacone as principal cusps. There is a distinct paraconule, but little or no trace of a metaconule. The stylar shelf is well developed, with a prominent anterolabial parastyle contacting and functioning together with the metastyle on P^4. Anterior and posterior basal cingula are well developed, but there is only rarely a trace of a lingual cingulum connecting these (PU 14165 is the only specimen preserving any trace of a lingual cingulum). Two specimens preserve a faint ridge running down the back of the protocone (postprotocingulum) connecting with the posterior basal cingulum. Three other specimens lack any trace of this postprotocingulum. M^2 is smaller than M^1, with no large parastyle and a more reduced metacone.

The lower canine and lower cheek teeth of *P. schaffi* are best preserved in PU 19365 (holotype). The canine is large, with a high curving crown. It has a distinct curving anterior keel running from the base of the crown to the apex. P_1 is small, single-rooted, with a simple pointed crown. P_{2-4} are double-rooted. P_2 has a simple crown with an anteriorly positioned protoconid and a small posterior basal cusp (hypoconulid). P_3 is similar to P_2 but larger, with a small hypoconid between the protoconid and hypoconulid. There is no anterior basal cusp in front of the protoconid on either P_2 or P_3. The crown of P_4 has a distinct anterior basal cusp (paraconid), a large sectorial protoconid, a small but well developed hypoconid and a smaller posterior basal hypoconulid. The hypoconid is positioned slightly labially relative to the midline of P_4, but the talonid is not basined like that on P_4 of *Bryanictis.*

The trigonid of M_1 is moderately high and somewhat more open than that of other species of *Protictis.* The protoconid is the largest of the trigonid cusps, and the paraconid is equal in size or even slightly larger than the metaconid. Together these three cusps form a very nearly equilateral triangle when seen in occlusal view. There is a distinct anterolabial cingulid near the base of the trigonid. The talonid of M_1 is moderately broad and basined. The hypoconid is the largest talonid cusp on M_1, and the hypoconulid and entoconid are each slightly smaller. M_2 is a large tooth with a low trigonid. The protoconid and metaconid are equal in size, and the paraconid is slightly smaller. Together these cusps form an acute triangle with the protoconid at its apex. The talonid of M_2 is relatively long, and narrower than the trigonid. The hypoconid and hypoconulid are large and form a sectorial shearing crest. The entoconid is smaller, and only partially closes the medial wall of the talonid. Left and right dentaries articulate by a long, shallow mandibular symphysis, which remains unfused throughout ontogeny. As in other species of *Protictis*, mental foramina are present below P_1 and P_3.

The basicranium is well preserved in PU 16495 (Fig. 11), a mature individual with moderately worn cheek teeth. No trace of an ectotympanic is preserved in this specimen, nor is there any trace of an auditory bulla. Consequently, it is not possible to determine to what extent the bulla may have been ossified. The promontorium of the petrosal is broad and flat, tapering anteriorly. The fenestra rotunda and fenestra ovale are well preserved on the posterolateral and lateral margins of the promontorium. The medial edge of the promontorium is rugose in texture suggesting cartilaginous articulation with an auditory bulla of some kind, whatever its composition. There is a large, well defined canal for the inferior petrosal sinus (Wible, 1983; medial branch of the internal carotid artery by interpretation of Matthew, 1909) traversing the lateral margin of the sphenoid, partially overlain by the petrosal on each side of the skull. This is best shown on the right side of the skull, where the petrosal no longer covers this canal. A groove for the stapedial branch of the internal carotid artery is clearly preserved on both petrosals in front of the fenestra rotunda and just below the point where this artery traversed the fenestra ovale, penetrating the

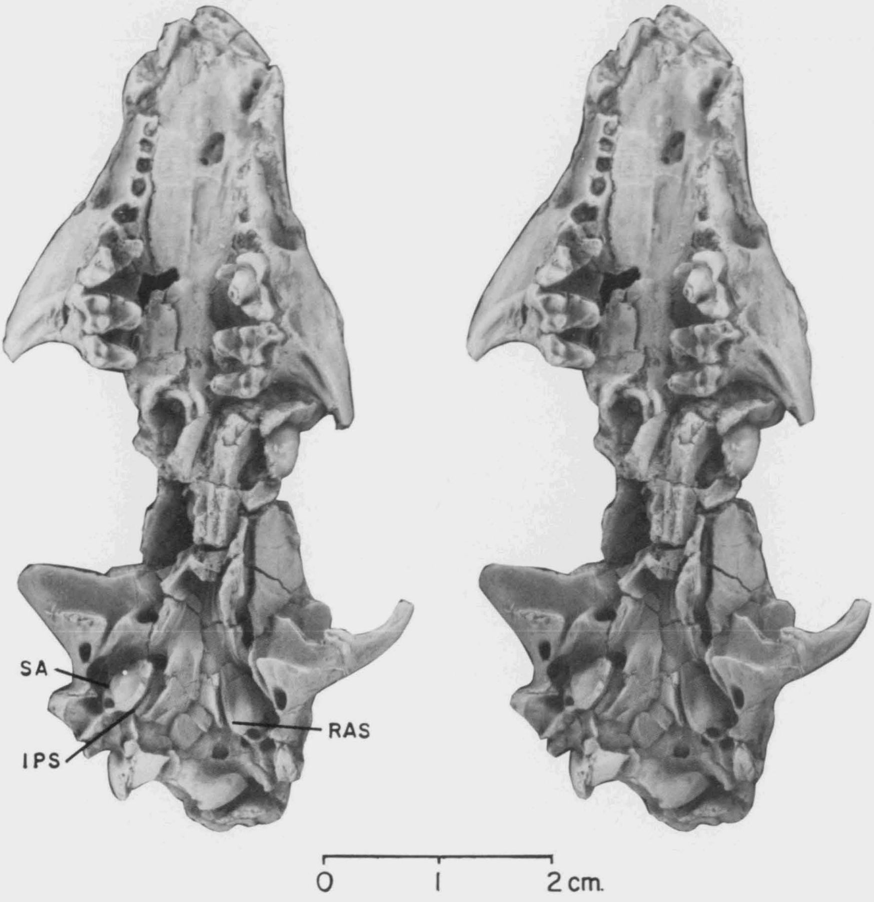

FIG. 11— Cranium of *Protictis schaffi* (PU 16495) from Princeton Quarry (late Tiffanian) in the Clark's Fork Basin, Wyoming. Stereophotograph showing palate with left P^4-M^2, right P^4 (part) and M^{1-2}, and slightly distorted basicranium, all in ventral view. Note groove for a large inferior petrosal sinus (*IPS*) positioned medial to the auditory bulla, and rugose articular surface (*RAS*) along medial edge of the petrosal delimiting medial margin of auditory bulla (bulla itself, ossified or unossified, is not preserved). The ventral surface of the promontorium of the left petrosal (at right in photographs) exhibits a faint groove that probably represents the promontory branch of the internal carotid artery. Apparent deep groove on ventral surface of the right petrosal is a preservational artifact. Note also groove for a small lateral stapedial artery (*SA*) crossing the fenestra ovale. Interpretation of carotid circulation follows Wible (1983). Scale 1.5 times natural size.

stapes (not preserved). A much fainter impression of a groove is present running anteriorly across the ventrolateral surface of the promontorium. This groove probably represents the promontory branch of the internal carotid artery (Wible, 1983, and personal communication).

Measurements of the holotype are as follows: $C_1L = 3.0$, $W = 2.0$; $P_1L = 1.5$, $W = 0.9$; $P_3L = 3.7$, $W = 1.6$; $P_4L = 5.3$, $W = 2.1$; $M_1L = 5.3$, $AW = 3.6$, $PW = 3.1$, $TL = 3.5$, $TH = 5.9$; mandibular depth below $M_1 = 7.6$. Measurements of the combined sample of all late Tiffanian *Protictis schaffi* are summarized in Table 7.

TABLE 7 — Summary of measurements of upper and lower cheek teeth of late Tiffanian *Proticiis schaffi* from Princeton Quarry, Schaff Quarry, and vicinity, Clark's Fork Basin, Wyoming. Measurements are defined in Figure 1. Abbreviations as in Table 1.

Tooth position		N	OR	$\overline{X}$	S	V
Upper dentition						
P^2	L	1	2.8	-	-	-
	W	1	1.2	-	-	-
P^3	L	1	4.1	-	-	-
	W	1	1.8	-	-	-
P^4	L	6	5.9 - 7.0	6.40	0.38	6.0
	W	6	3.8 - 4.5	4.10	0.25	6.2
M^1	L	7	4.0 - 4.7	4.50	0.23	5.1
	AW	7	6.2 - 7.1	6.56	0.29	4.4
	PW	7	5.5 - 6.2	5.74	0.23	4.0
	TL	7	2.8 - 3.3	3.03	0.17	5.6
M^2	L	4	2.7 - 3.0	2.85	0.13	4.5
	W	3	4.9 - 5.5	5.18	0.28	5.3
Lower dentition						
C_1	L	1	3.0	3.00	-	-
	W	2	2.0 - 2.2	2.15	-	-
P_1	L	1	1.5	-	-	-
	W	1	0.9	-	-	-
P_2	L	-	-	-	-	-
	W	-	-	-	-	-
P_3	L	3	3.2 - 3.7	3.43	0.25	7.3
	W	3	1.4 - 1.6	1.50	0.10	6.7
P_4	L	5	4.7 - 5.4	5.04	0.33	6.5
	W	5	2.0 - 2.2	2.08	0.08	4.0
M_1	L	8	5.2 - 5.7	5.36	0.15	2.8
	AW	10	3.4 - 3.7	3.51	0.10	2.8
	PW	9	2.8 - 3.4	3.01	0.18	5.9
	TL	9	3.3 - 3.6	3.41	0.11	3.1
	TH	6	5.4 - 5.9	5.70	0.21	3.7
M_2	L	2	4.6 - 4.8	4.70	-	-
	AW	2	2.6 - 3.0	2.80	-	-
	PW	2	2.2 - 2.3	2.25	-	-
	TH	2	2.5 - 3.0	2.75	-	-
Mand. depth		7	6.4 - 7.8	7.16	0.55	7.7

Discussion.—The configuration of cranial arteries in primitive carnivores and other mammals can only be inferred from fossils, interpreted, to be sure, in light of living forms. The presence of a moderately large canal for a "medial internal carotid artery" in PU 16495, in addition to a faint groove for the promontory branch of the internal carotid artery and a clearly defined groove for a distinct stapedial branch of the carotid artery, might appear to support Matthew's (1909, p. 358) inference that three branches of the internal carotid artery were present in middle Eocene *Viverravus* and other primitive mammals. On the other hand, an early Eocene skull of *Viverravus acutus* (UM 67326) currently under study shows no evidence of a promontory groove. Presley (1979) has questioned Matthew's configuration (three branches of the internal carotid appearing simultaneously), based on comparative study of the ontogeny of this anatomical region in living mammals. Furthermore, Wible's (1983) review of fossil evidence suggests that the "medial internal carotid artery" of Matthew (1909) and others is really an inferior petrosal sinus. Consequently, there is now little basis for interpreting the groove medial to the promontorium in *Protictis* (or in *Viverravus*) as part of the internal carotid arterial system.

Radinsky (1977) described the flattened partial endocast of the brain of PU 16495 (as "*Didymictis*"), noting that the neocortex is little expanded, lacking sulci, and the inferior (posterior) colliculi of the corpora quadrigemina are equal in size to the superior (anterior) colliculi. Sensory and motor association functions of the neocortex were presumably somewhat less well developed than those of later carnivores. The superior colliculi serve as centers for visual reflexes, and the inferior colliculi serve as centers for acoustic reflexes. The fact that both are similar in size in *Protictis schaffi* may indicate that vision and audition were of comparable importance in this Paleocene predator.

Typodigm.—Three specimens are known from the type locality, Schaff Quarry: PU 19365 (holotype, L dent. P_2-M_1, R dent. C_1-P_1P_3-M_2), 19391 (L max. P^4-M^1), and 19476 (L max. P^4-^{1}). Referred specimens are known from Princeton Quarry (SC-187): PU 13964 (R max. P^2-M^1), 14165 (L max. P^4-M^2), 14315 (L dent. M_1), 14318 (R dent. M_1), 14441 (R max. P^4-M^2) 16495 (skull with palate and basicranium), 17848 (L dent. C_1P_{3-2}), 17849 (L dent. P_3-M_2), 17853 (L iso. P^4), UM 68855 (L dent. M_1), and 76857 (L dent. M_{1-2}); Northwest of Princeton Quarry: PU 18955 (R max. P^4-M^2); Storm Quarry: PU 18318 (L dent. P_4-M_2); Fossil Hollow (SC-198): PU 22015 (R iso. M_1); SC-165: UM 68271 (R iso. M_1), 69538 (L max. M^{1-2}), 81709 (L iso. P_4); and SC-270: UM 73577 (L iso. M_1). UM 73360 from SC-257, at or near the Tiffanian-Clarkforkian boundary, is slightly larger than any other specimen of this species but it is clearly closely related.

Protictis agastor n. sp.

Fig. 12

Protictis cf. *haydenianus*, Rose, 1981, p. 152.

Holotype.—PU 21311, left dentary with M_{1-2}.

Type locality.—Cedar Point Quarry, Fort Union Formation in northern Bighorn Basin, Wyoming.

Age and distribution.—Middle Tiffanian Land-Mammal Age (late Paleocene) in the northern Bighorn Basin, Wyoming.

Diagnosis.—Differs from *Protictis paralus*, *P. laytoni*, and *P. schaffi* in being significantly larger (ca. 71%, 105% or 32% larger, respectively, in linear dimensions). Differs from these species and *P. haydenianus* in having a longer and more massive trigonid on M_2. Differs from *P. dellensis* in being significantly smaller (ca. 13% smaller in linear dimensions).

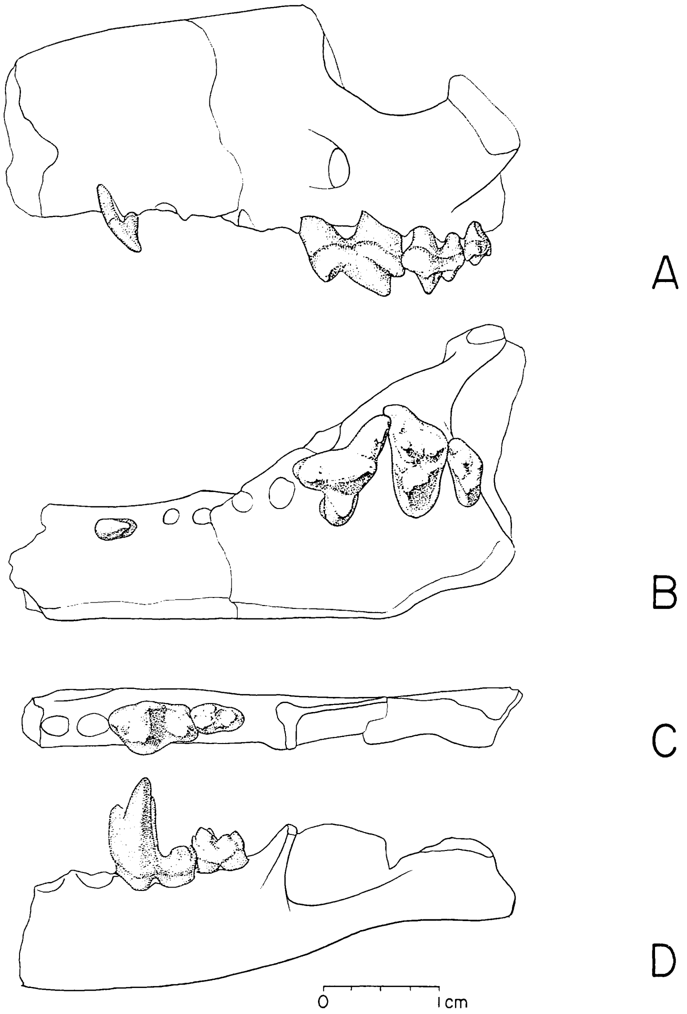

FIG. 12— Upper and lower dentition of *Protictis agastor* from Cedar Point Quarry (middle Tiffanian) in the northern Bighorn Basin, Wyoming. A-B, left maxilla with P^1 and P^4-M^2 (PU 21242) in lateral (A) and occlusal (B) view. C-D, left dentary with M_{1-2} (holotype, PU 21311) in occlusal (C) and lateral (D) view. Note high trigonid on M_1 and anteroposteriorly elongated trigonid with bulbous cusps on crushing crown of M_2 characteristic of this species and *P. dellensis*.

Etymology.—agastor, Greek, kinsman, in allusion to the close relationship inferred for this species and *Protictis dellensis*.

Description.—One good maxilla, PU 21242, is known from the type locality. It preserves a large alveolus for the upper canine. P^1 is two-rooted, with a single apical cusp and a simple labiolingually compressed crown. Judging from alveoli, P^{2-3} were both double-rooted. P^4 is similar in form to that in *P. schaffi*, differing only in having a larger, more medially positioned protocone and a larger more inflated anterior parastyle. M^1 and M^2 are also similar in form to these teeth in *P. schaffi*. On M^1, all of the cusps are slightly higher and at the same time blunter. There is no lingual cingulum on M^1. The crown of M^2 is relatively smaller than that in *P. schaffi*.

UM 64555 is a dentary of *P. agastor* with alveoli for the lower canine, a single-rooted P_1, double-rooted dP_2 or P_2, and crowns of P_3 and P_4 erupting. P_3 appears to be erupting ahead of P_4. Mental foramina are located beneath the sites of definitive P_1 and P_3. The most complete dentary of this species is PU 21311 (holotype), with alveoli for P_4 and intact crowns of M_{1-2}. The crown of M_1 is similar in size and proportion to that in *P. haydenianus*, with a large high protoconid, moderately large paracone and metacone approximately equal in size, and a basined talonid of moderate width. M_2 is distinctive in being relatively small, with a large equilateral trigonid and narrow basined talonid. The trigonid is larger, relative to the talonid, the trigonid cusps are more bulbous, and the talonid is narrower than comparable features in *P. haydenianus*.

Measurements of the type specimen, PU 21311, are as follows: $M_1L = 6.5$, $AW = 4.4$, $PW = 3.4$, $TL = 4.3$, $TH = 8.3$; $M_2L = 4.3$, $AW = 2.7$, $PW = 2.2$, $TH = 3.1$. Mandibular depth below $M_1 = 9.1$. Measurements of the entire sample of this species from Cedar Point Quarry are summarized in Table 8.

Discussion.—We conservatively interpret both larger and smaller forms of large *Protictis* from Cedar Point as males and females, respectively, of a single species *Protictis agastor*. The holotype is one of the group of smaller individuals. Should it prove likely that two species of large *Protictis* are represented at this locality, *P. agastor* would apply to the smaller. The group of specimens including the holotype of *Protictis agastor* is, in any event, clearly different from *P. dellensis*.

Typodigm.—The following specimens are known from the type locality, Cedar Point Quarry: PU 19983 (L dent. M_2), 21242 (L max. P^1P^4-M^2), 21311 (holotype, L dent. M_{1-2}), 22011 in part (two L iso. M_1s, R M_1 trigonid, R dent. P_4), UM 63102 (M_1, sacrificed for strontium analysis), 64555 (R dent. P_{3-4} erupting), 71836 (L iso. M_1).

Protictis dellensis (Dorr, 1952)

Fig. 13

Didymictis dellensis Dorr, 1952, p. 85, fig. 6, Pl. 7, figs. 3, 4.
Didymictis ?sp. nov., Rose, 1981, p. 156.

Holotype.—UM 27232, right dentary with C_1-P_1 and P_3-M_2.

Type locality.—Dell Creek Quarry, Hoback Formation, Hoback Basin of western Wyoming.

Age and Distribution.—Late Tiffanian Land-Mammal Age (late Paleocene). This species is known from localities in the northern Bighorn Basin and Clark's Fork Basin, Wyoming, in addition to the type locality.

Diagnosis.—Largest species of *Protictis*. Differs from *P. haydenianus*, *P. paralus*, *P. laytoni*, and *P. schaffi* in being significantly larger and in having a larger, more massive trigonid on M_2. Differs from *P. agastor* in being significantly larger.

Description.—PU 13961 and 14319 (possibly representing the same individual) together constitute most of a right maxilla. Alveoli indicate that P^{1-3} were all double-rooted. The crown of P^4 is similar to that in *P. agastor*, although the anterior parastyle is clearly smaller than the protocone in this species. M^1 and preserved remains of M^2 are larger (and more worn), but otherwise very similar to M^{1-2} in known *P. agastor*.

UM 27232 (holotype) is still the most complete dentary of this species, and it is the only specimen known preserving the lower canine. As in *P. schaffi*, the canine has an anteromedial crest or keel running from the base to the apex of the crown. P_1 is single-rooted, with a labiolingually compressed crown, a simple apical cusp, and a small posterior cuspule. P_2 is two-

TABLE 8 — Summary of measurements of upper and lower cheek teeth of middle Tiffanian *Protictis agastor* from Cedar Point Quarry, northern Bighorn Basin, Wyoming. Measurements are defined in Figure 1. Abbreviations as in Table 1.

Tooth position		N	OR	$\bar{X}$	S	V
Upper dentition						
P^1	L	1	3.0	-	-	-
	W	1	1.6	-	-	-
P^2	L	-	-	-	-	-
	W	-	-	-	-	-
P^3	L	-	-	-	-	-
	W	-	-	-	-	-
P^4	L	1	9.1	-	-	-
	W	1	6.5	-	-	-
M^1	L	1	5.5	-	-	-
	AW	1	8.9	-	-	-
	PW	1	7.8	-	-	-
	TL	1	4.1	-	-	-
M^2	L	1	5.5	-	-	-
	W	1	2.8	-	-	-
Lower dentition						
P_4	L	1	7.8	-	-	-
	W	1	3.3	-	-	-
M_1	L	5	6.5 - 7.5	7.06	0.38	5.4
	AW	6	4.2 - 5.5	4.80	0.49	10.3
	PW	4	3.4 - 4.1	3.75	0.29	7.7
	TL	5	3.3 - 4.5	4.20	0.51	12.1
	TH	4	8.3 - 8.9	8.55	0.30	3.5
M_2	L	2	4.3 - 5.1	4.70	-	-
	AW	2	2.7 - 2.9	2.80	-	-
	PW	2	2.2 - 2.6	2.40	-	-
	TH	2	3.1 - 3.2	3.15	-	-
Mand. depth		2	9.1 -14.8	11.95	-	-

rooted, and the crown (preserved in PU 13937) is long and narrow, with a simple apical cusp and a small posterior cuspule. P_3 and P_4 are double-rooted and similar in form. Both have long narrow crowns, an anteriorly positioned basal paraconid, a large compressed protoconid, smaller accessory hypoconid, and a crest-like posterior basal hypoconulid. There is a faint posterolingual cingulid on both premolars, better developed on P_4, making the talonids of both teeth slightly basined. The crown of M_1 is large, with a massive trigonid and broadly basined talonid. The paraconid and metaconid are approximately equal in size, making an acute angle with the more prominent protoconid. As in *P. agastor*, the trigonid of M_2 is open, with bulbous crushing cusps, and the talonid is basined but narrow.

The mandibular symphysis is long, shallow, and unfused in *P. dellensis* as it is in other *Protictis*. The holotype, UM 27232, preserves four mental foramina on the lateral surface of the

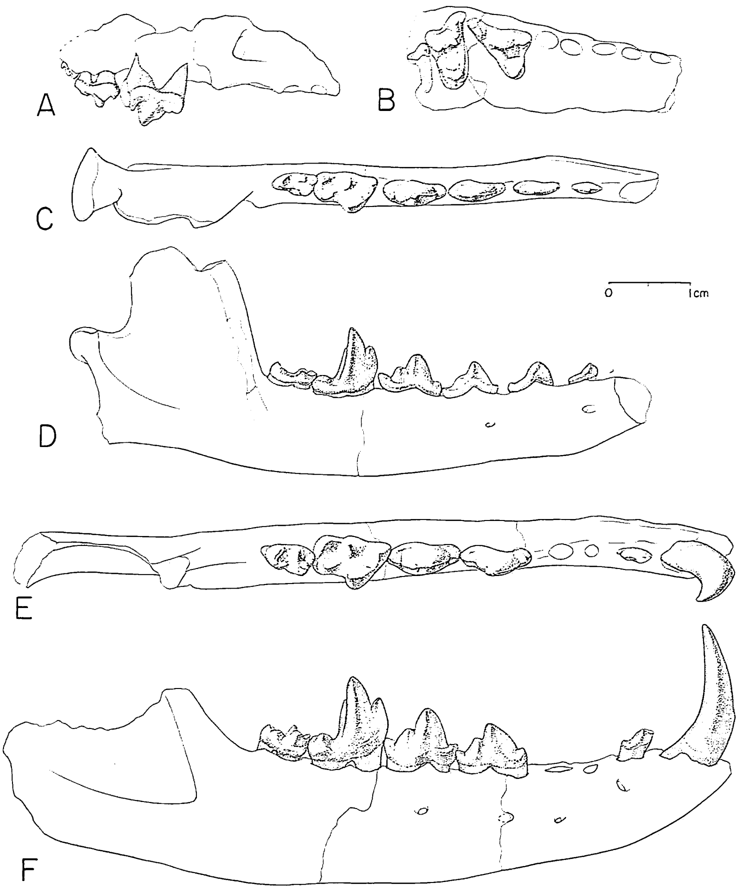

FIG. 13— Upper dentition of *Protictis dellensis* from Princeton Quarry. A-B, right maxilla with P^4, M^{1-2} (PU 14319, 13961) in lateral (A) and occlusal (B) views. Lower dentition of putative female and male *Protictis dellensis* from Princeton Quarry in the Clark's Fork Basin and Dell Creek Quarry in the Hoback Basin, Wyoming. C-D, right dentary with P_1-M_2 from Princeton Quarry (PU 13937) in occlusal (C) and lateral (D) view. E-F, right dentary with C_1-P_1 and P_3-M_2 from Dell Creek Quarry (holotype, UM 27232) in occlusal (E) and lateral (F) view. Note difference in overall size of these specimens suggesting sexual dimorphism, and anteroposteriorly elongated trigonid with bulbous cusps on crushing crown of M_2 characteristic of this species and *P. agastor*. High trigonid of M_1 and narrow talonid on M_2 distinguish *Protictis* from later *Didymictis*.

dentary, one below each premolar. PU 13937, on the other hand, has the typical *Protictis* pattern of two mental foramina, one beneath both P_1 and P_3. The masseteric fossa is well preserved in both of these specimens, and in both it is very deeply excavated. The mandibular condyle in PU 13937 is cylindrical, with the articular surface wrapping around the ventral part of the posteromedial part of this cylinder.

Measurements of the type specimen, UM 27232, are as follows: $C_1L = 5.3$, $W = 3.4$; $P_1L = 3.8$, $W = 1.7$; $P_3L = 8.5$, $W = 3.2$; $P_4L = 9.0$, $W = 3.9$; $M_1L = 8.5$, $AW = 6.1$, $PW = 4.8$, $TL = 5.2$, $TH = 9.6$; $M_2L = 6.1$, $AW = 4.0$, $PW = 3.1$, $TH = 3.3$. Mandibular depth beneath $M_1 = 14.2$. Measurements of all of the known specimens of this species are summarized in Table 9.

TABLE 9 — Summary of measurements of upper and lower cheek teeth of late Tiffanian *Protictis dellensis* from Princeton Quarry and vicinity in the Clark's Fork Basin and Dell Creek Quarry in the Hoback Basin, Wyoming. Measurements are defined in Figure 1. Abbreviations as in Table 1.

Tooth position		N	OR	$\bar{x}$	S	V
Upper dentition						
P^3	L	1	7.2	-	-	-
	W	1	3.5	-	-	-
P^4	L	2	8.4 - 8.7	8.55	-	-
	W	3	6.1 - 7.6	6.73	0.78	11.5
M^1	L	1	6.0	-	-	-
	AW	1	9.0	-	-	-
	PW	1	7.9	-	-	-
	TL	1	4.3	-	-	-
Lower dentition						
C_1	L	1	5.3	-	-	-
	W	1	3.4	-	-	-
P_1	L	2	3.8	3.80	-	-
	W	2	1.4 - 1.7	1.55	-	-
P_2	L	1	5.8	-	-	-
	W	1	1.8	-	-	-
P_3	L	2	7.3 - 8.5	-	-	-
	W	2	2.6 - 3.2	-	-	-
P_4	L	2	8.1 - 9.0	8.55	-	-
	W	2	3.4 - 3.9	3.65	-	-
M_1	L	3	7.5 - 8.5	8.10	0.53	6.5
	AW	3	5.0 - 6.1	5.60	0.56	9.9
	PW	3	4.0 - 4.8	4.47	0.42	9.3
	TL	3	4.7 - 5.5	5.13	0.40	7.9
	TH	3	8.5 - 9.7	9.27	0.67	7.2
M_2	L	3	5.5 - 6.1	5.70	0.35	6.1
	AW	3	3.2 - 4.0	3.53	0.42	11.8
	PW	3	2.4 - 3.1	2.80	0.36	12.9
	TH	2	2.8 - 3.3	3.05	-	-
Mand. depth		2	10.2 -14.2	12.20	-	-

Discussion.—*Protictis dellensis* was originally described as a species of *Didymictis* (as were most *Protictis*). Of all *Protictis*, this species is most similar to later *Didymictis*, at least in size. However, *P. dellensis* has a relatively shorter trigon on M^1, higher trigonid and narrower talonid on M_1, and a higher, more open trigonid and narrower talonid on M_2, characteristics that clearly ally it with *Protictis* rather than *Didymictis*. *P. dellensis* may prove to be ancestral to later *Didymictis*, but it has not yet acquired the diagnostic features of this genus.

UM 27232 and PU 13937 are here interpreted as male and female of the same species. They could as well represent different species. One way to test these alternative interpretations is to analyze the pattern of tooth size variability in larger samples of *Didymictis* as these become available from Clarkforkian and Wasatchian localities. If *Didymictis* should prove to be a direct descendant of *Protictis agastor* and *P. dellensis*, then patterns of variability observed in *Didymictis* could appropriately be applied in interpreting *Protictis* as well. Pending new information, we conservatively retain both large and small forms in a single species *P. dellensis*.

Typodigm.—Two specimens are known from the type locality, Dell Creek Quarry: UM 27232 (holotype, R dent. $C_1P_1P_3$-M_2), and 27526 (L iso. P^{3-4}). Referred specimens are known from Divide Quarry: UM 63281 (R iso. M_1); Princeton Quarry: PU 13937 (R dent. P_1-M_2), 13961 (R max. P^4), 14317 (L iso. M_1, probably same individual as 13937), 14319 (R max. M^1), 14320 (L iso. P^4); and Fossil Hollow (SC-198): UM 69241 (L dent. M_{1-2}, weathered) and 80249 (R iso. M_2).

Intyrictis n. gen.

Protictis (*Bryanictis*) (in part), MacIntyre, 1966, p. 190.
Bryanictis (in part), Rigby, 1980, p. 84.

Type species.—*Protictis* (*Bryanictis*) *vanvaleni* MacIntyre 1966.

Included species.—Type species only.

Age and distribution.—*Intyrictis* is known from the Torrejonian Land-Mammal Age (middle Paleocene) of New Mexico and southwestern Wyoming. It has not been found in the Torrejonian of northwestern Wyoming or Montana.

Diagnosis.—Resembles *Bryanictis* in having a relatively lower crowned P_4 and a lower trigonid on M_1 compared with other Viverravidae. Differs from *Bryanictis* and all other viverravid genera in having a prominent metaconid on P_4.

Etymology.—Named for Dr. Giles Ternan MacIntyre, in recognition of his major contribution to the study of Paleocene Viverravidae.

Discussion.—As long as the holotype was the only known specimen, it was impossible to know if this medium-sized viverravid represented a taxon different from *Bryanictis microlestes*, or merely an aberrant individual of that species. Rigby (1980) has recently reported a large collection of "*Bryanictis*" *vanvaleni* from Swain Quarry in southwestern Wyoming. This collection includes 24 P_4s, which, according to Rigby, all have a well defined metaconid. None of the specimens of *Bryanictis* (or any other viverravid) examined in the course of our study showed any trace of a metaconid on P_4. Consequently, we here place "*Bryanictis*" *vanvaleni* in a new genus *Intyrictis*. The consistency with which the metaconid is developed in *Intyrictis* indicates that this form is quite different from other known viverravids, one probably confined to more southerly latitudes than those being sampled in northern Wyoming and Montana.

Intyrictis vanvaleni (MacIntyre, 1966)

Protictis (*Bryanictis*) *vanvaleni* MacIntyre, 1966, p. 190, fig. 20, Pl. 16, fig. 6, Pl. 17, figs. 5, 8, Pl. 18, fig. 1.
Bryanictis vanvaleni, Rigby, 1980, p. 84.

Holotype.—AMNH 16031, left dentary with P_4 and partial M_1.

Type locality.—East fork of Arroyo Torrejon, Nacimiento Formation, San Juan Basin, New Mexico.

Age and distribution.—Torrejonian Land-Mammal Age (middle Paleocene) of northern New Mexico and southwestern Wyoming.

Diagnosis.—As for the genus.

Description.—All known specimens of this species are described by MacIntyre (1966) and Rigby (1980). This species is not known from Gidley Quarry or Rock Bench Quarry.

Typodigm.—The only specimen known from the type locality is AMNH 16031 (holotype). Other referred specimens from Swain Quarry in southwestern Wyoming include AMNH 87921a-k, 87925, 87926, 87927a-b, 87928a-j, 87930a-f, 88071a-j, 88076a-h, 88078a-h, 88079(?), 88081a-d(?), 88082, 88083a-e, 100368, 100380a-g, 100440a-h, 100448a-d, 100451, 100593, 100594, 100602, 100603a-b, 100608, 100609, 100610, 100629, 100631, 100633a-e, 100634, 100635, 100637a-e, 100697a-b, 100784a-c, 100797a-b, and 100825 (Rigby,1980, p. 85).

Raphictis n. gen.

Type species.—*Raphictis gausion* n. sp.

Included species.—Type species only.

Age and distribution.—Middle Tiffanian Land-Mammal Age (late Paleocene) of northwestern Wyoming.

Diagnosis.—Differs from all other viverravid genera in having relatively narrower lower cheek teeth, and higher, more needlelike trigonid cusps on M_1. Also differs in having the talonid of M_1 set at an angle relative to both the trigonid and the long axis of the dentary.

Etymology.—*Raphis*, Gr., needle, and *iktis*, Gr. (fem.), martin or weasel, in reference to the sharp needlelike trigonid of M_1 in this genus, and its inferred weasel-like habits.

Discussion.—Features distinguishing *Raphictis* are not found in any other North American viverravid. Chinese *Pappictidops acies* Wang (1978), a species that is rather different from the type species of *Pappictidops* (*P. orientalis* Qiu and Li, 1977), resembles the type species of *Raphictis* to some degree in having very narrow lower premolars and molars. "*P.*" *acies* could conceivably represent an Asian species of *Raphictis*.

Raphictis gausion n. sp.
Fig. 14

Protictis sp., Rose, 1981, p. 152.

Holotype.—PU 21244, left dentary with P_3-M_2.

Type locality.—Cedar Point Quarry, Fort Union Formation, northern Bighorn Basin, Wyoming.

Age and distribution.—Middle Tiffanian Land-Mammal Age (late Paleocene). This species is known only from the type locality.

Diagnosis.—As for the genus.

Etymology.—*gausos*, Gr., angled, bent (with a comparative suffix), in reference to the more angled position of the talonid on M_1, relative to both the trigonid and long axis of the dentary, distinguishing this species from other viverravids.

Description.—The upper dentition of *Raphictis* is not yet known. The lower dentition is best preserved in PU 21244 (holotype), where the canine and P_1 are represented by incomplete alveoli. P_2 is represented by an additional pair of alveoli. The crown of P_3 is preserved intact in PU 19987. It is narrow, with a single apical cusp (protoconid), and a small posterior basal hypoconulid.

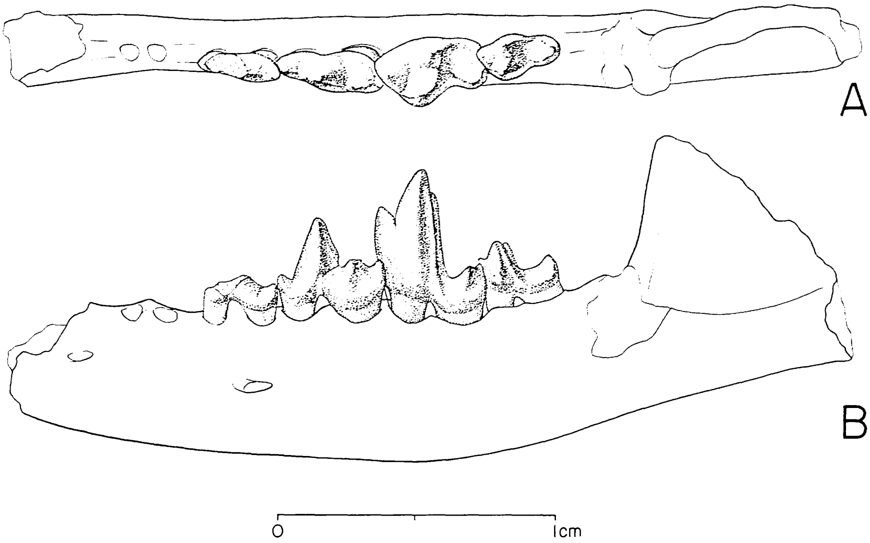

FIG. 14— Lower dentition of *Raphictis gausion* from Cedar Point Quarry (middle Tiffanian) of northern Bighorn Basin, Wyoming. Left dentary with P_3-M_2 (holotype, PU 21244) in occlusal (A) and lateral (B) view. Note narrow crowns of all teeth and obliquely angled talonid on M_1 characteristic of this genus.

There is no trace of an anterior basal cusp, nor is there any trace of an accessory hypoconid behind the protoconid. P_4 is preserved in three specimens, including the holotype. It too has a narrow crown with a large compressed protoconid and small posterior hypoconulid. In addition, P_4 has an anterior basal paraconid, and a distinct hypoconid behind and slightly labial to the protoconid. There is no lingual cingulid, and the talonid of P_4 is unbasined.

The trigonid and talonid of M_1 are both relatively narrow by comparison with those of *Protictis*. The protoconid on M_1 is high and sharp. The paraconid is nearly as high as the metaconid, and it is more centrally located on the midline of the tooth (and dentary) than is typical of *Protictis*. The paraconid, protoconid, and metaconid together form an approximately equilateral triangle. The talonid of M_1 is moderate in width and somewhat basined. It differs from that in other viverravid species in being more oblique relative to the trigonid and long axis of the dentary, the entire talonid appearing to be rotated several degrees labially. This appearance is enhanced by reduction of the entoconid and lingual edge of the talonid. M_2 is small and narrow, with a moderately high and open trigonid, but a long, narrow, slightly basined talonid. The hypoconid and entoconid are more reduced on M_2 in *Raphictis* than they are in other Paleocene viverravids.

The mandibular symphysis is long, shallow, and unfused in the holotype. Mental foramina are located below P_1 and P_3, as in other viverravids.

Measurements of the holotype are as follows: $P_3L = 2.8$, $W = 1.0$; $P_4L = 4.0$, $W = 1.5$; $M_1L = 3.4$, $AW = 2.4$, $PW = 1.8$, $TL = 2.4$, $TH = 4.5$; $M_2L = 2.9$, $AW = 1.5$, $PW = 1.1$, $TH = 1.9$. Mandibular depth below $M_1 = 5.1$. Measurements of the entire sample of this species from Cedar Point Quarry are summarized in Table 10.

Typodigm.—The following specimens are known from the type locality, Cedar Point Quarry: PU 19987 (R dent. P_3-M_1), 21244 (holotype, L dent. P_3-M_2), 22011 in part (R iso. M_1, L iso. M_1, and L iso M_1 trigonid), and UM 64639 in part (L iso. P_4).

TABLE 10 Summary of measurements of lower cheek teeth of middle Tiffanian *Raphictis gausion* from Cedar Point Quarry, northern Bighorn Basin, Wyoming. Measurements are defined in Figure 1. Abbreviations as in Table 1.

Tooth position		N	OR	$\bar{X}$	S	V
Lower dentition						
P_3	L	2	2.7 - 2.8	2.75	-	-
	W	2	1.0 - 1.2	1.10	-	-
P_4	L	3	4.0 - 4.5	4.17	0.29	6.9
	W	3	1.5 - 1.8	1.67	0.15	9.2
M_1	L	4	3.4 - 3.9	3.70	0.22	5.8
	AW	5	2.4 - 2.6	2.48	0.08	3.4
	PW	4	1.6 - 2.0	1.83	0.17	9.4
	TL	5	2.3 - 2.6	2.48	0.13	5.3
	TH	5	4.0 - 4.9	4.64	0.24	5.2
M_2	L	1	2.9	-	-	-
	AW	1	1.5	-	-	-
	PW	1	1.1	-	-	-
	TH	1	1.9	-	-	-
Mand. depth		2	5.1 - 5.8	5.45	-	-

DISCUSSION

In beginning this study, we considered each of the principal quarry samples of middle and late Paleocene viverravids separately, showing that four viverravid species are present at Rock Bench Quarry, three species are probably present at Cedar Point Quarry, and three species are probably represented at Princeton Quarry and vicinity. Within each quarry sample, individual species can most easily be distinguished on the basis of overall size (Figs. 2-4). Other morphological characteristics of Paleocene viverravids are consistent with, and further support, initial distinctions based on size. Any consideration of the evolution of Viverravidae through time requires temporal ordering of samples, which is, in this study, provided by stratigraphic superposition and a dense network of faunal correlations within the northern Bighorn Basin and adjacent Clark's Fork Basin. The stratigraphic distribution of tooth size, and by inference body size, in successive samples of Paleocene Viverravidae is shown in Figure 15. This chart and the morphological comparisons detailed above suggest a tentative outline of the phylogenetic relationships of early North American viverravids.

Ictidopappus mustelinus is a highly specialized viverravid known only from the Torrejonian Land-Mammal Age (middle Paleocene) of Montana. It is not yet known from the Bighorn Basin. The two species of *Simpsonictis* present in the Bighorn Basin, *S. tenuis* and *S. pegus*, are very similar and undoubtedly closely related. They too are known only from the Torrejonian. *Bryanictis microlestes* may be closely related to *Intyrictis vanvaleni*, a species not represented in existing collections from the Bighorn, Clark's Fork, or Crazy Mountain basins. Both of these genera and species are restricted to the Torrejonian. A fifth genus present in the Torrejonian, *Protictis*, ranges from New Mexico through Wyoming and Montana. It is more generalized than *Ictidopappus*, *Simpsonictis*, *Bryanictis*, or *Intyrictis*, and Torrejonian *Protictis* is the most

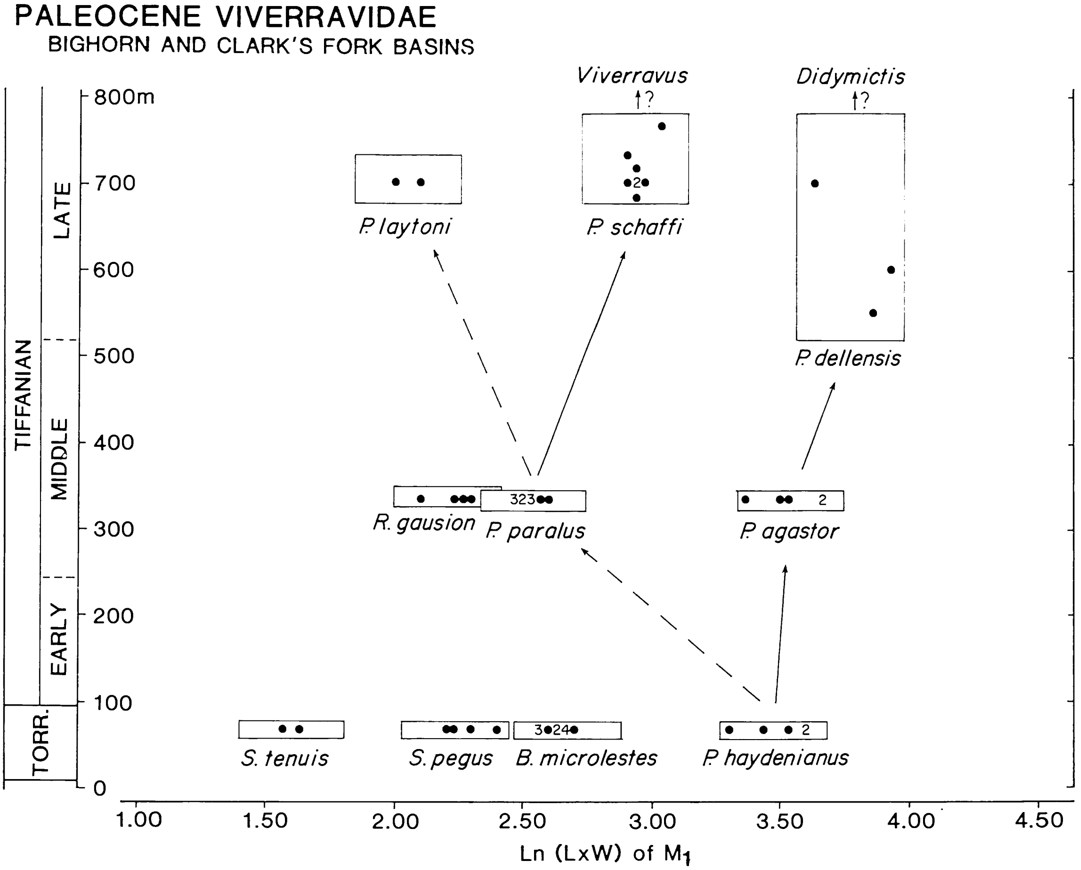

FIG. 15 — Stratigraphic and possible phylogenetic relationships of Paleocene Viverravidae in the Bighorn and Clark's Fork basins, Wyoming. Abscissa measures tooth size and, by inference, body size. Ordinate is stratigraphic level (in meters) above the base of the Fort Union Formation on Polecat Bench. Torrejonian Rock Bench Quarry is at the 60 m level, middle Tiffanian Cedar Point Quarry is at approximately 325 m, and late Tiffanian Princeton Quarry is at the 700 m level. *Simpsonictis*, *Bryanictis*, and *Raphictis* appear to have very restricted stratigraphic ranges, while *Protictis* ranges from the Torrejonian through the Tiffanian. Torrejonian *Ictidopappus* and *Intyrictis* are not known from the Bighorn or Clark's Fork basins and consequently they are not shown here. Pattern of stratophenetic linking is based on all morphological characteristics preserved in the specimens at hand. Note apparent asymmetry in evolution of *Protictis*, with large *P. haydenianus* giving rise to small, medium, and large species in later intervals. *Protictis schaffi* is a likely ancestor of some or all later *Viverravus*. *P. dellensis* is a plausible ancestor of later *Didymictis*, but *Bryanictis* also resembles *Didymictis* in the proportions of its upper and lower molars. *Bryanictis* may be ancestral to *Didymictis* in spite of the absence of known Tiffanian intermediates.

plausible common ancestor for all of the known Tiffanian viverravids. Two distinct lineages of *Protictis* are represented in the middle Tiffanian, and three distinct lineages are represented in the late Tiffanian. In addition, the divergently specialized genus *Raphictis* is likely to be derived from Torrejonian *Protictis*. Derivation from *Simpsonictis* is also possible, but *Raphictis* does not have the triangular P_4 (in occlusal outline), reduced paraconid on M_1, or high trigonid on M_2 characteristic of *Simpsonictis*.

There is, as shown here, considerable diversity in middle Paleocene Viverravidae. Five genera and six species are known from sediments of Torrejonian age in the Western Interior of North

America. This great diversity suggests that viverravids probably evolved in North America in the early Paleocene, although there is as yet very little direct evidence of this (see MacIntyre, 1966, p. 146). Species of *Pappictidops* described from the Paleocene of China indicate that viverravids were not restricted geographically to North America, but their diversity in Asian faunas is so restricted that it is unlikely Viverravidae radiated widely there.

The central problem motivating this study, relationship of Eocene *Viverravus* and *Didymictis* to Paleocene Viverravidae, is only partially clarified here. *Viverravus* and *Didymictis* themselves require thorough revision. The dentition of late Tiffanian *Protictis schaffi* is similar to that of Clarkforkian *Viverravus politus* and, as Rose (1981, p. 157) noted, *P. schaffi* is likely to be the direct ancestor of *Viverravus politus* (and possibly other species of this genus as well). *P. schaffi* differs from *V. politus* in retaining a slightly higher protoconid and less open trigonid on M_1, and it differs in having a more triangular (less rectangular) trigonid on M_2, differences of degree normally associated with the transition from one species to another. The differences between successive species *Protictis haydenianus* and *P. paralus*, or *P. paralus* and *P. schaffi*, within the genus *Protictis* are just as great.

Tiffanian *Protictis dellensis* is a possible ancestor for Clarkforkian and later *Didymictis*. *Protictis dellensis* is a relatively large species like all known species of *Didymictis*, however *P. dellensis* has a relatively shorter trigon on M^1, a higher trigonid and narrower talonid on M_1, and a higher, more open trigonid and narrower talonid on M_2, features in which it differs from *Didymictis*. Torrejonian *Bryanictis* has a relatively long trigon on M^1, trigonids of moderate height on $M_{1\text{-}2}$, and broad lower molar talonids, features in which it resembles *Didymictis*. Multivariate analysis of lower molar measurements (summarized in the accompanying tables) together with similar measurements of representative Clarkforkian *Viverravus* and *Didymictis* separated species initially on the basis of overall size (principal component I) and secondarily on the basis of trigonid height and talonid narrowness (the measure of shape reflected by principal component II). *Bryanictis* and *Didymictis* appear to be most similar in molar shape among Paleocene and early Eocene viverravids. It is possible that *Didymictis* evolved from *Bryanictis* rather than *Protictis*. If so, this apparently happened outside the geographic range of known late Paleocene mammalian faunas, possibly in Asia or possibly somewhere in the southern part of North America, and transitional forms are unknown. Any definitive statement regarding the ancestry of *Viverravus* and *Didymictis* must await careful systematic review of Clarkforkian and Wasatchian Viverravidae.

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