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ANCESTRY AND SPECIES DEFINITION IN PALEONTOLOGY: A STRATOCLADISTIC ANALYSIS OF PALEOCENE-EOCENE VIVERRAVIDAE (MAMMALIA, CARNIVORA) FROM WYOMING

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PAUL DAVID POLLY[1]

Abstract—The ability to distinguish between terminal taxa and those that form a continuous lineage is important for most paleobiological enterprises, including documentation of patterns of diversity, extinction, and morphological change through time. Especially in cases with a dense fossil record containing closely related species, conventional cladistic analysis is not adequate for this task because *a priori* judgments about the monophyly or paraphyly of operational taxonomic units are impossible. Even when a fossil taxon contains an autapomorphy, it is impossible to test its monophyly using cladistic analysis without resorting to assumptions about the irreversibility of evolution.

Stratocladistics offers solutions to these problems because it operates in the universe of phylogenetic trees rather than cladograms—the monophyly and paraphyly of taxa are determined as a result of analysis rather than included as assumptions. This is possible because the basic units of analysis are lineage segments rather then lineages and because Fisher's *total parsimony debt* allows the evaluation of hypotheses that alternatively place a taxon in a terminal position or as part of a continuous lineage.

This, in turn, allows species definitions such as Simpson's evolutionary species to be operationalized in a cladistic framework. The definition of a species-level taxon can be separated from its morphological diagnosis using a formula like the following: a species is the set of ancestor-descendant populations that occurred between speciation (cladogenic) events. Typological problems associated with many morphological species definitions, including those relying on autapomorphies, are thus avoided.

This method is applied to a revision of Clarkforkian and Wasatchian viverravid carnivorans from the Bighorn and Clarks Fork basins, Wyoming. It is concluded that seven species, one new, were present: *Viverravus laytoni*, *V. acutus*, *V. rosei* (sp. nov.), *V. politus*, *Didymictis proteus*, *D. leptomylus*, and *D. protenus*. The species *Protictis laytoni* is referred to the genus *Viverravus* and synonymized with *V. bowni*. Furthermore, *P. dellensis* is found to be conspecific with *D. proteus* and the two are synonymized under the latter name. For the same reason, *P. schaffi* is synonymized with *V. politus*. The taxon Didymictida is rejected. The species *V. acutus* is concluded to be sexually dimorphic with high variability in linear measurements of its dentition.

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INTRODUCTION

Populations directly ancestral to others, however rare, undoubtedly exist in the known fossil record (Foote, 1996). This is especially apparent when paleontological species—which have a stratigraphic range and are, therefore, presumed to be a series of ancestor-descendant populations[2] —are considered (Imbrie, 1957; Fisher, 1992, 1991; Rose and Bown, 1993). An epistemological paradox is posed by the existence of ancestral populations, however, because of the recent convention of treating ancestors as if they are unknown or unknowable. When cladistics is applied to fossil taxa, it is often done under the assumption, with little or no empirical justification, that no taxon in the analysis is directly ancestral to any other—all taxa are treated as though they were terminal branches. If phylogenetic analysis is viewed only as a tool for creating a cladistic classification based on recency of common ancestry, this assumption is not particularly problematic.

If, however, the goal of analysis is a phylogenetic framework for studies of evolutionary patterns and processes, then the distinction between those fossil populations that are ancestral to others and those that are not is imperative. Studies of diversity through time, patterns of extinction, modes of speciation, rates of evolution, and morphologic change all depend on accurate distinctions between lineages that become extinct and those that continue to evolve and diversify (Gingerich, 1983a; Smith and Patterson, 1988; Benton, 1989; Badgley, 1990; Fisher, 1991; Harvey and Pagel, 1991; Norell, 1992, 1993; Smith, 1994). Except in the trivial case in which all taxa are contemporaneous, it is impossible, using traditional cladistic analysis, to determine whether a given taxon is actually a terminal branch or ancestral to other taxa. Yet the documentation of many evolutionary patterns depends on this distinction because terminal taxa imply extinction, whereas ancestral taxa imply temporal continuity. In this paper, stratocladistic analysis, which provides a rigorous method for distinguishing ancestral taxa from terminal taxa (Fisher, 1991, 1992, 1994), is applied to Paleocene-Eocene viverravid carnivore material from the Bighorn and Clarks Fork basins of Wyoming. The result is a well-informed, explicit phylogeny, which can serve as an appropriate basis for further evolutionary studies.

Cladistics and the case against ancestry.—In spite of a general lack of enthusiasm for the concept of ancestors in the cladistic literature, a set of three standards for their identification has been put forward (Engelmann and Wiley, 1977; Eldredge and Cracraft, 1980; Schoch, 1986; Smith, 1994). An ancestor is: (1) expected to possess synapomorphies that unite it with its putative descendants; (2) expected not to have autapomorphies of its own, nor synapomorphies that unite it with some, but not all of its descendants; and (3) expected to have lived before its descendants. These criteria appear eminently logical: synapomorphies document the ancestor's close relationship to its descendants; autapomorphies would indicate that the taxon was not an ancestor, but a monophyletic terminal taxon (Donoghue, 1985); and direct ancestors occur before their descendants—anachronisms are not ancestors.

Yet these criteria, especially the second, have subtleties that led systematists to reject them as insufficient and to exclude the concept of ancestry from phylogenetic analysis. Unlike their living counterparts, taxa in the fossil record may be ancestral to later occurring taxa, even though they have features that appear to be autapomorphies (Eldredge and Cracraft, 1980).

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[2] Throughout this paper (unless otherwise specified) the term "ancestor" refers to a population (in its broad sense of a reproductively cohesive set of contemporaneous individuals) from which other such populations are descended. Thus, an ancestor is an instantaneous—with all the caveats that must apply when using that term geologically—segment within a single paleontological or evolutionary species (see Rose and Bown, 1993 for a recent review of these concepts). In this paper, "ancestor" is meant to be a very specific term and does not refer to an evolutionary species that persists alongside its daughter species nor does it refer to an ancestral higher taxon (although both of these usages are quite plausible). See Smith (1994) for a discussion of different usages of the term "ancestor".

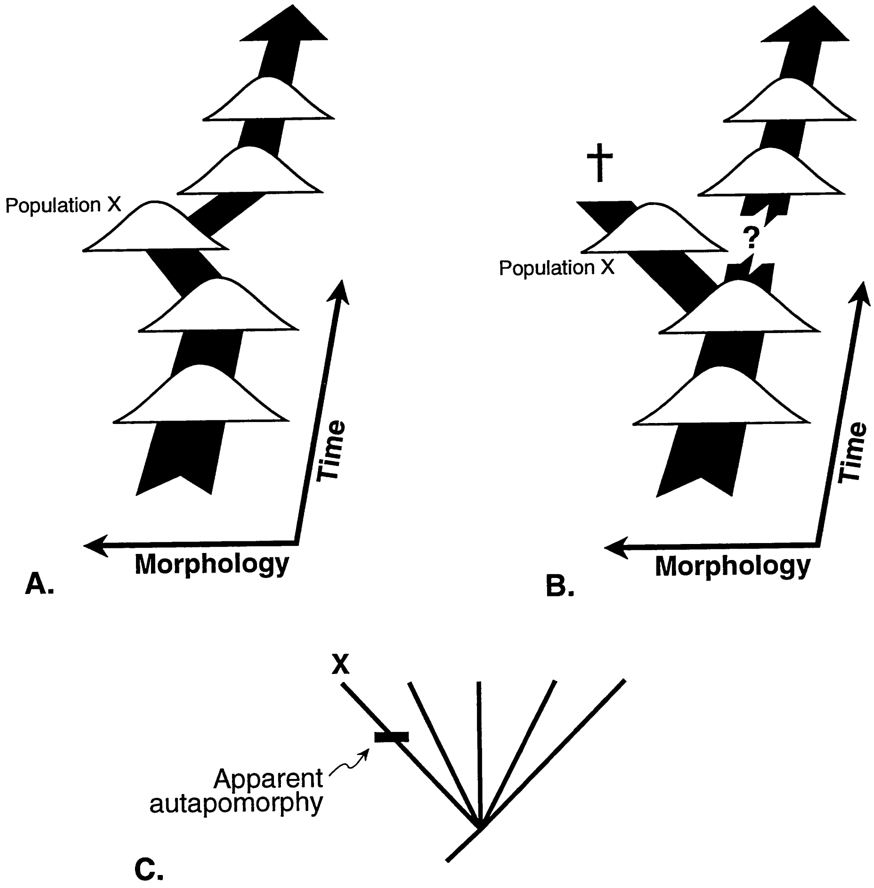


FIG. 1—Alternative interpretations of successive population samples in the fossil record. A, interpretation as a lineage in which morphologic change occurs and is subsequently reversed. B, alternative interpretation with a branching event producing two lineages, one of which (population X) becomes extinct. C, cladogram consistent with both scenarios. Population X seems to possess an autapomorphy: traditional cladistic analysis, which relies only on morphological data, favors scenario B because it only invokes one character-state change; but stratocladistic analysis, which utilizes both morphologic and stratigraphic evidence, favors A and B equally because A requires two character-state changes but no instances of stratigraphic non-preservation, while B requires one character-state change and one instance of stratigraphic non-preservation. ? = hypothesis of stratigraphic non-preservation. † = extinction of lineage.

This situation occurs when characters are gained and lost during the evolution of a single, unbranched lineage (Fig. 1A). Early segments of such a lineage appear to have derived features that are not shared with later segments. Traditional morphological parsimony criteria dictate that scenario 1B is to be preferred over 1A; the former scenario requires only one character state change—the acquisition of an autapomorphy—while the latter requires two state changes—an acquisition and subsequent loss.

However, in order for a systematist to make the argument that the most parsimonious solution (1B) more accurately represents phylogeny than does the less parsimonious solution (1A), the postulate must be invoked that character reversal does not occur in evolution (Eldredge and Cracraft, 1980). If one is to argue that Population X (Fig. 1B) is really a monophyletic unit which left no descendant populations, then one has to argue that populations without the autapomorphy found in Population X cannot be descended from X. "If autapomorphies are sufficient to reject the hypothesis of ancestry, there is an implicit assumption that a particular autapomorphy cannot revert to its 'primitive' condition" (Eldredge and Cracraft, 1980: 136). Because most systematists were unwilling to make such an assumption, they chose instead the seemingly more palatable solution that hypotheses of ancestry were untestable (Engelmann and Wiley, 1977; Eldredge and Cracraft, 1980; but see Gingerich, 1976; Szalay, 1977.). Without recourse to more powerful methods, systematists retreated from the onerous world of phylogenetic trees and ancestor-descendant relationships to a glib cosmos of cladograms and recency-of-common-ancestry.

Stratocladistics and the case for ancestry.—This choice was made, however, under the presumption that morphological character distributions are the only data amenable to parsimony analysis. Since that time, the concept of stratigraphic parsimony has broadened the horizon of possibilities. Stratigraphic data offer a previously lacking temporal component, which, in conjunction with morphological data, allows the systematist to operate in the universe of phylogenetic trees rather than cladograms. Stratocladistics (Fisher, 1991, 1992, 1994) is an analytical method that makes use of both morphological and stratigraphic data. It is parsimony-based in that it favors the phylogenetic hypothesis with the minimal number of *ad hoc* statements; it differs from cladistics in that it seeks to minimize both morphologic and stratigraphic *ad hoc* statements. To do this, it relies on a measurement called *total parsimony debt* (Fisher, 1992)—the phylogenetic hypothesis favored in a stratocladistic analysis is the one which minimizes total debt by invoking fewest instances of homoplasy and/or cases of stratigraphic non-preservation.

Using the *total parsimony debt* criterion, both of the phylogenetic interpretations in Figure 1 are equally parsimonious, because each contains the same number of *ad hoc* hypotheses. The interpretation in Figure 1A requires an hypothesis of character reversal, which is morphologically less parsimonious than an hypothesis in which the character only arose once and Population X is monophyletic. However, the hypothesis in Figure 1B requires an hypothesis of stratigraphic non-preservation, because the removal of Population X to a side-branch leaves a stratigraphic gap in the main lineage. In this case, there is a tension between the morphologic and stratigraphic data that prevents either hypothesis from being favored (see Fisher, 1992 for details on the calculation of *total parsimony debt*). Significantly, if Population X did not have an autapomorphy, then the *total parsimony debt* criterion would favor the interpretation that Population X is ancestral to later segments.

Using stratocladistics as a tool by which to judge competing hypotheses, systematists may now move back into the universe of phylogenetic trees. This is a methodological triumph because of the high probability of encountering ancestral taxa in the fossil record and because of the importance that their correct interpretation holds for our reconstruction of historical patterns and processes. The direct mapping of phylogenetic analysis onto phylogeny also allows us to simplify our terminology. Complex and circumspect locutions for possible ancestral taxa—'metaspecies', 'metataxa', 'ambitaxa', and the rest (Donoghue, 1985; Gauthier et al., 1988; de Queiroz and Donoghue, 1988; Archibald, 1994)—are no longer necessary if the methodological impasse of ancestry has indeed been breached. These terms and their associated concepts are only necessary because of the ambiguity of mapping cladograms to phylogenetic trees and because of the difficulty in distinguishing between ancestor-descendant and sister-group relationships.

Definition and diagnosis of fossil species.—Testable hypotheses of ancestry and descent also allow new solutions to old problems surrounding species definition in the fossil record. In any one time horizon, boundaries between species are often discrete (although this is a gross oversimplification) and can be recognized as reproductively or morphologically (in the case of fossil material) distinct populations. However, if we could reverse time, we would see populations that are reproductively isolated transform and merge as we step back generation by generation. Each time slice contains transient species (Imbrie, 1957) that are the descendants of their predecessors and, sometimes, ancestors of progeny.

Yet because of variability and evolutionary change, there is no necessary resemblance, either in morphology or number, between transient species from one time slice and those from another. The ubiquitous and continuous nature of variation and change make species extremely difficult to define using morphological features (Simpson, 1951, 1953; Ghiselin, 1984; Gingerich, 1991a; Rose and Bown, 1993). This means that as our knowledge of evolutionary intermediates between and of variation within named species increases, their scope and definition require continual revision. Name-bearing type specimens ensure that the names of taxa are stable (Stoll et al., 1961). But species boundaries remain linked to a particular author's knowledge of temporal and spatial variation and most nomenclatorial synonymy remains subjective (perhaps rightly so).

Nevertheless, various attempts have been made to clarify the intended scope of taxonomic groups by separating their definition—the rules for delimiting them within a phylogenetic continuum—from their diagnosis—the features by which they can actually be recognized (Rowe, 1987, 1988; de Queiroz, 1992; de Queiroz and Gauthier, 1992). This is done by framing the definition of a taxon in terms of ancestry, leaving the morphological diagnosis and determination of constituency to analysis and revision. In its usual formulation (but see Polly, 1996) a taxon is defined as the last common ancestor of two or more 'types' and all of the descendants of that ancestor. The goal is to tie the names of higher taxa to definitional formulae in order to provide nomenclatorial stability and a (relatively) objective means for determining synonymy.

This method has not been readily applicable to species level taxa because triangulation cannot be used to identify a single ancestor. The genealogical plexus created by sexual reproduction means that two individual organisms within a species level taxon have many ancestors in common in a way that two species or higher taxa do not. However, a paleontological species can be thought of as a lineage—a series of morphologically (and presumably reproductively) isolated populations that are part of an ancestor-descendant sequence; indeed, virtually all versions of the species concept in paleontology use this model (*e.g.*, Imbrie, 1957; Hennig, 1966; Gingerich, 1976; Fisher, 1991; Rose and Bown, 1993; Lister, 1993). We can thus create a definitional formula for a species—*the set of ancestor-descendant populations that form a continuous series between two arbitrary boundaries*—which can be named by choosing a name-bearing holotype from its members. An hypothetical example of such a construction would be that Species X is the series of ancestor-descendant populations which contains the holotype X and which is bounded by speciation (cladogenic) events.

While species may be crisply defined in this way, their membership may be difficult to determine in practice. Among other things, the extension of such a definition must be based upon a phylogenetic hypothesis containing both branching events and ancestor-descendant relationships. Traditional cladistic analysis includes an hypothesis of branching order, but is inadequate for testing ancestor-descendant relationships. This definitional formula can, however, be used in conjunction with analyses that operate explicitly within the realm of phylogenetic trees (*e.g.*, Gingerich, 1976; Fisher, 1991, 1993, 1994; Smith, 1994). It can also accommodate many (but not all) species concepts that have been applied to the fossil record: evolutionary species (Simpson, 1961; Wiley, 1978), cladistic species (Westoll, 1956; Hennig, 1966; Ridley, 1989), chronospecies (Simpson, 1961; Gingerich, 1976; Rose and Bown, 1993), or species delimited so as to have no greater range of morphological variability than is found in living species (Gingerich, 1976; Rose and Bown, 1993).

As has often been pointed out, the beginning and end of all of these types of species is arbitrary (*e.g.*, Simpson, 1961; Gingerich, 1976; Rieppel, 1986; Rose and Bown, 1993). Whether at a branching event, at a point when a suitable degree of morphological change has accumulated, or at a point when the direction of change shifts, species boundaries must always be drawn between a parent and offspring generation and are arbitrary in that sense. In this paper, I have chosen to arbitrarily divide species at cladogenic events. This, in effect, makes the concept of speciation in the fossil record equivalent to most neontological usages of the term speciation, the breakdown of a single reproductively isolated population into two or more. While terminological synonymy is a clear advantage, there are some disadvantages to this procedure: anagenesis may result in early members of a species looking quite different from later members (masking potentially valuable biostratigraphic information), early members of a species may be morphologically similar to members of both the parent- and sister-species, and populations from particular stratigraphic intervals may be shifted from one species to another as hypotheses of phylogenetic branching order change (Rose and Bown, 1993). No matter what species concept one adopts, there are tradeoffs in information content. The only disadvantage that I consider particularly damning is the loss of biostratigraphic data by subsuming morphological change within a species name. To counteract this, I have presented measurement data for each species as a whole and for each stratigraphic sub-unit.

The present study is unusual in that species-level taxa are identified after phylogenetic analysis rather than before. Rose and Bown (1993) rightly pointed out that several currently advocated species concepts require knowledge of phylogenetic relationships before they can be applied. This procedure allows many of the attributes of a species—such as its stratigraphic range, level of variability, and rate of evolutionary change—to be measured rather than prescribed by its definition. Fisher (1992:125) argued that "any attribution of a stratigraphic range to a taxon is a substantive statement of relationship between earlier- and later-occurring representatives and should be the result of an analysis rather than part of the input." Stratocladistic analysis and the explicit testing of ancestor-descendant relationships between populations from different stratigraphic intervals make this possible. It is also possible to determine the monophyly or paraphyly of a population or species as the result of analysis rather than requiring it as an *a priori* assumption as does cladistic methodology.

MATERIALS AND METHODS

Stratocladistic analysis was used to revise the late Paleocene and early Eocene viverravids from the Bighorn and Clarks Fork basins. The University of Michigan Museum of Paleontology collection includes more than 450 individual specimens collected from ten successive faunal zones (Cf-1 through Cf-3 and Wa-0 through Wa-6). Several lineages of viverravids are represented in this collection, each of which evolved and diversified through Clarkforkian and Wasatchian time; the detailed stratigraphic data associated with UM localities and the large number of specimens make this an appropriate venue for a phylogenetic reconstruction technique that distinguishes between ancestor-descendant and sister-group relationships. Some of the material described below was previously studied by Bown (1979) and Rose (1981), but the majority is treated here for the first time. The current project complements and extends that of Gingerich and Winkler (1985), who analyzed the Torrejonian and Tiffanian viverravids from the Bighorn and Clarks Fork basins.

Dental measurements.—Dental measurements were taken from material housed in the University of Michigan and American Museum of Natural History collections. Lengths and widths of the posterior premolars and molars were measured on all 431 specimens. In addition, the lengths, widths, and heights of molar trigonids were measured on specimens in faunal zones Wa-2 and Wa-3. Measurements are those described by Gingerich and Winkler (1985). Comparative dental measurements were taken from three species of extant carnivorans following Gingerich and Winkler (1979). Lengths and widths of all teeth and the heights of upper and lower canines were taken from 42 individuals of *Urocyon cinereoargenteus* (the gray fox), 61 individuals of *Martes americana* (the American marten), and 108 individuals of *Mustela frenata* (the long-tailed weasel). All of these specimens are housed in the University of Michigan Museum of Zoology. Measurements of both fossil and recent specimens were taken with Mitotuyo digital calipers to the nearest 0.1 millimeter.

Operational phylogenetic units.—Specimens were divided into operational phylogenetic units or OPUs, in Fisher's nomenclature, for stratocladistic analysis. An OPU, the basic unit of a phylogenetic analysis, is a temporally restricted lineage segment which may or may not be ancestral to other such units. These were identified by first dividing the fossil sample stratigraphically and then sorting individuals into morphologically disjunct groups within each interval (Smith, 1994).

In order to maximize the number of individuals in each cluster, stratigraphic horizons were lumped by faunal zone. This is by no means the most detailed stratigraphic data available for Bighorn and Clarks Fork basin material, but the use of such detailed stratigraphic resolution would have resulted in only one or two specimens from each interval. For purposes of this analysis, specimens assigned to an individual faunal zone were treated as though they came from an instantaneous time horizon. This is, of course, not true and it should be recognized that these are lumped samples; any events that appear to happen at the boundaries of faunal zones probably happened more gradually within that zone. A plot of specimens of *Viverravus acutus* (one of the best represented species identified by this analysis) by meter level (Fig. 2) indicates that neither apparent diversity nor range of variability are distorted by lumping specimens by faunal zone. Information on localities and stratigraphic levels was obtained from UM catalogues, except for the McCullough Peaks area, which was provided by William Clyde. Philip Gingerich provided locality and stratigraphic information for AMNH type specimens. Faunal zone ages follow Gingerich (1983b, 1989, 1991b), Clyde et al. (1994), and Woodburne and Swisher (1995).

Within each faunal zone specimens were grouped into morphologically disjunct clusters by applying multivariate discrimination techniques to the dental measurement data. In most cases, the length and widths of the lower first molar seemed adequate for discriminating samples (Gingerich, 1974, 1976), but in all cases multivariate analysis of all of the measurements were used to identify OPUs. In general, of a series of bivariate analyses were carried out, one for each tooth, of log transformed data. Clusters from each analysis were collated using individual specimens with associated teeth. The efficacy of this method was partially verified by applying principal components ordination to specimens from faunal zones Wa-2 and Wa-3, which were the only zones with a sufficient number of specimens containing complete cheek tooth rows. The two methods identified the same OPUs in each of these two zones. While the possibility of morphologically identical sibling species always exists, there is ample evidence to suggest that these statistically discriminated groups represent samples from reproductively isolated groups (Allen, 1938; Simpson, 1941, 1951; Kurtén, 1953; Colbert and Hooijer, 1953; Imbrie, 1957; Doyen and Slobodchikoff, 1974; Gingerich, 1974, 1976; Yablakov, 1974; Gingerich and Winkler, 1985; Cope and Lacy, 1995; Suchentrunk and Flux, 1996).

Stratocladistic analysis.—Discrete character states for 39 morphological characters (Appendix 1) were scored for each OPU, as is routine in cladistic analysis. The characters were partially drawn from recent literature on viverravids (Flynn and Galiano, 1982; Gingerich and Winkler, 1985; Fox and Youzwyshyn, 1994), but were supplemented by characters chosen after comparative analysis of the fossil material. The ancestral or primitive state in Viverravidae was hypothesized for each character by treating *Cimolestes cerberoides*, *Palaeoryctes puercensis*, and *Ravenictis krausei* as outgroups (Maddison et al., 1984). To reduce computation time, an hypothetical taxon consisting of the primitive state of each character was used as a proxy for the three outgroups in the phylogenetic data matrix. When more than one character state was present among the individuals of a single OPU, the most derived was chosen (Mabee and Humphries, 1993; Murphy,1993; Wiens, 1995). A stratigraphic character was also coded for each OPU. A total of 15 stratigraphic levels were used: Torrejonian, early Tiffanian, middle Tiffanian, late Tiffanian, Cf-1, Cf-2, Cf-3, Wa-0,

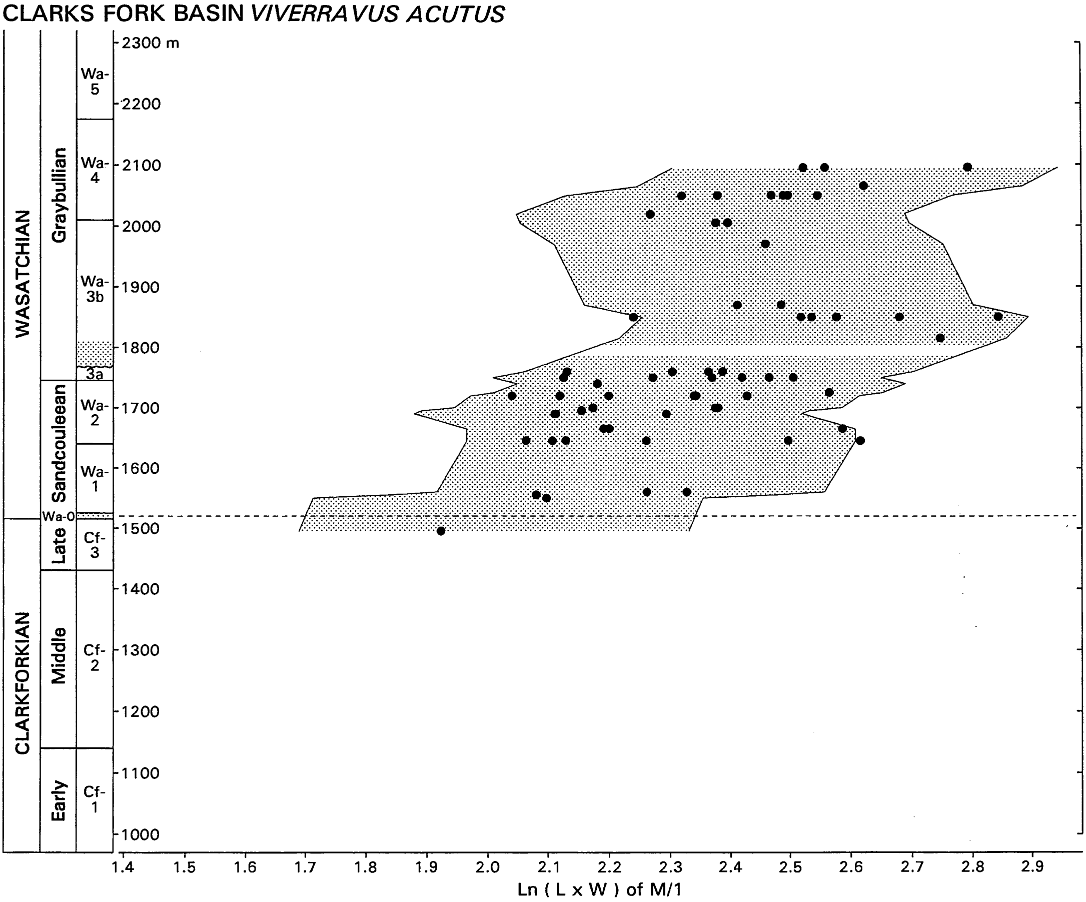


FIG. 2—Stratigraphic distribution of specimens referred to *Viverravus acutus* in this study. Specimens are plotted by meter level here to show that general trends in size and directional change are similar when the data are grouped by meter level or faunal zone (cf. Fig. 7). Specimens were grouped by faunal zone in this study so that those from localities in the Bighorn and Clarks Fork basins could be merged, even though they come from different stratigraphic sections.

Wa-1, Wa-2, Wa-3, Wa-4, Wa-5, and Wa-6, which were coded 0 through D respectively. The complete data matrix used in this analysis is found in Appendix 2.

Following the procedure recommended by Fisher (1992), a set of morphologically most-parsimonious cladograms was used as the starting point for identifying the phylogenetic trees with the least total parsimony debt. Cladograms were identified using PAUP (Swofford, 1990). Before performing the cladistic search on PAUP, safe taxonomic reduction methods were used to remove redundant OPUs (Wilkinson, 1995A, 1995B; Wilkinson and Benton, 1996). Inclusion of redundant taxa do not affect the overall topology of a cladogram, but simply increase the number of most parsimonious trees. All taxa were considered when total parsimony debt was assessed, and all appear in the final phylogenetic trees. It should be noted that there is currently no available computer algorithm for minimizing total parsimony debt and that the shortest stratocladistic tree is not guaranteed to be consistent with any of the morphologically most-parsimonious cladograms (Fisher, 1992). MacClade (Maddison and Maddison, 1992) was used to identify the shortest phylogenetic trees. This program is useful because it calculates a tree-length based on both morphologic and stratigraphic characters (Fisher, 1992). It also contains a 'make ancestor' tool, which was used to collapse taxa to ancestral positions. Each subset of most-parsimonious cladograms with low stratigraphic tree-lengths was manipulated in this manner to identify the phylogenetic tree with the lowest total parsimony debt.

Species identification.—Species were identified only after arriving at the final phylogenetic hypothesis. These were delimited on the tree using the following defining formula: *a species is the set of ancestor-descendant populations that occurred between speciation (cladogenic) events*. Names were applied to these species using the standard rules of nomenclature—if a species had one or more named holotypes within its boundaries, the name with priority was used. If there was no named holotype within its boundaries, a new name was coined and a holotype designated. It should be noted that names were assigned to taxa only after the phylogenetic analysis. For clarity, I refer to taxa throughout the paper using the names applied to them *a posteriori*, in most cases using both a Latin binomial and a faunal zone designation.

Summary.—The entire procedure is summarized in Figure 3. Operational Phylogenetic Units (OPUs) were identified by using multivariate discrimination techniques on each stratigraphic sample (Fig. 3A). Morphological characteristics were scored for each OPU and most-parsimonious cladograms were generated using these data (Fig. 3B). Both morphologic and stratigraphic data were used to generate a phylogenetic hypothesis that contained the fewest number of *ad hoc* statements, either about character evolution or stratigraphic non-preservation (Fig. 3C). The morphologically most-parsimonious cladograms were used as a starting point for this search. Finally, species were delimited on the phylogenetic tree and names were applied to these.

RESULTS

Identification of OPUs.—Thirty-two OPUs were identified. Summary statistics for each are reported in the Systematic Paleontology section. For clarity, these are referred to throughout using species names assigned to them at the end of the analysis. Most of the OPUs are easily identifiable in Figure 4, which is a series of bivariate plots—one for each faunal zone—of the length and width of the lower first molar of each specimen. Gingerich (1974, 1976) argued that the areal dimension of M_1 is usually sufficient to sort individuals from closely related sympatric species into their respective taxa (although it should be made clear that he did not argue that only such data should be used). This study confirmed that in most cases M_1 is sufficient. But in the Wa-2 sample, M_1 dimensions did not separate specimens belonging to *Viverravus politus* from those belonging to *Didymictis leptomylus* (Fig. 4). However, the morphology of M_1, both dimensional and morphologic data from other teeth, and the results of the phylogenetic analysis clearly separate individuals belonging to these two taxa. It is recommended that as much data as possible be used when identifying taxa.

Sexual dimorphism in Viverravus acutus.—In most cases, the range of variation in each OPU is similar to that reported in living species. Previous investigations suggested that the typical range of variation for linear measurements of mammalian teeth is about 0.20 units on a natural-logarithmic scale, while areal measurements typically have a range of about 0.40 units on a natural-log scale (Gingerich, 1974, 1976; Gingerich and Winkler, 1979; Pengilly, 1984). All of the *Didymictis* clusters (Fig. 4) have size ranges similar to those of the extant foxes *Vulpes vulpes* and *Urocyon cinereoargenteus* (Gingerich and Winkler, 1979; Pengilly, 1984; Fig. 5). However, the *Viverravus acutus* clusters in Wa-1 through Wa-5 are more variable than the fox species and have a range of between 0.40 and 0.50 units on a natural log scale. Gingerich and Winkler (1985) reported that size variability was higher in sexually dimorphic species such that linear measurements had a range of 0.30-0.40 on a logarithmic scale. This was confirmed by

TABLE 1—Summary of measurements of the upper and lower cheek teeth of *Martes americana* from British Columbia. This species is sexually dimorphic, with males being larger, on average, than females. All measurements in millimeters.

Tooth position	N	Observed range	Mean	Standard deviation	Coefficient of variation
Upper dentition					
P^4 L	121	6.38 - 9.16	7.76	0.5483	7.06
W	121	4.06 - 5.82	4.86	0.4425	9.11
M^1 L	120	3.36 - 5.56	4.51	0.5522	12.26
W	120	6.33 - 8.74	7.44	0.5752	7.73
Lower dentition					
P_4 L	119	4.58 - 6.44	5.55	0.3927	7.08
W	120	2.20 - 3.13	2.61	0.2137	8.19
M_1 L	121	7.71 - 10.10	8.84	0.6327	7.16
W	121	2.65 - 4.16	3.53	0.3021	8.55
M_2 L	120	2.06 - 3.66	2.84	0.3720	13.11
W	120	2.51 - 3.63	2.96	0.2789	9.42

the data collected on *Urocyon cinereoargenteus* (not particularly dimorphic), *Martes americana* (somewhat dimorphic), and *Mustela frenata* (extremely dimorphic)—these have average linear measurement ranges of 0.34, 0.43, and 0.56, respectively, in natural log units. It is plausible that *Viverravus acutus* exhibited sexual dimorphism of a magnitude similar to that of *Martes americana*, but less than that of *Mustela frenata*. Summary statistics for *M. americana* are presented in Table 1.

Phylogeny.—The strict consensus of the 1470 morphologically-most parsimonious cladograms identified by PAUP is presented in Figure 6A. Each equally parsimonious tree has a length, based exclusively on morphological characters, of 74 steps, a consistency index (CI) of 0.784, and a retention index (RI) of 0.914. This is the best estimate of cladistic relationships among the 23 non-redundant OPUs (eight of the original thirty-two were identified as redundant according to Wilkinson's safe taxonomic reduction techniques). The vast majority of the 1470 cladograms varied only in the placement of *Viverravus* OPUs relative to one to another.

Addition of stratigraphic data and application of Fisher's total parsimony debt criterion resulted in two equally parsimonious phylogenetic trees, which differ from one another only in the placement of *Protictis paralus* at an ancestral or terminal position (Fig. 6B). When only nonredundant taxa were included, these trees had total lengths of 91 steps. Of these, 74 steps were morphological (a debt of 16 steps) and 17 steps were stratigraphic. When the redundant OPUs were reinstated, the morphological debt remained the same, but the stratigraphic debt decreased to 3 steps: *Viverravus rosei* is unknown in Wa-0, *V. laytoni* is unknown in Cf-1, and there are no viverravids known at all in the early Tiffanian. Total parsimony debt for this analysis is, therefore, 20 steps.

The reason for the vast difference in the ability of cladistics and stratocladistics to resolve the relationships of these taxa is simple—the stratigraphic data rule out many combinations that are possible when morphology alone is considered. The *Viverravus* clade illustrates this best. Even though the OPUs making up this clade are not completely redundant in terms of cladistic information, they were closely related with few meristic character differences among them. In fact, the *V. acutus*, *V. rosei*, and *V. politus* OPUs are all segments of long lineages in which there was very little anagenetic change (Fig. 7). There was not enough morphological differentiation among them to allow a cladistic analysis to resolve their relationships. The addition of stratigraphic data, however, quickly demonstrates that these taxa form only a few

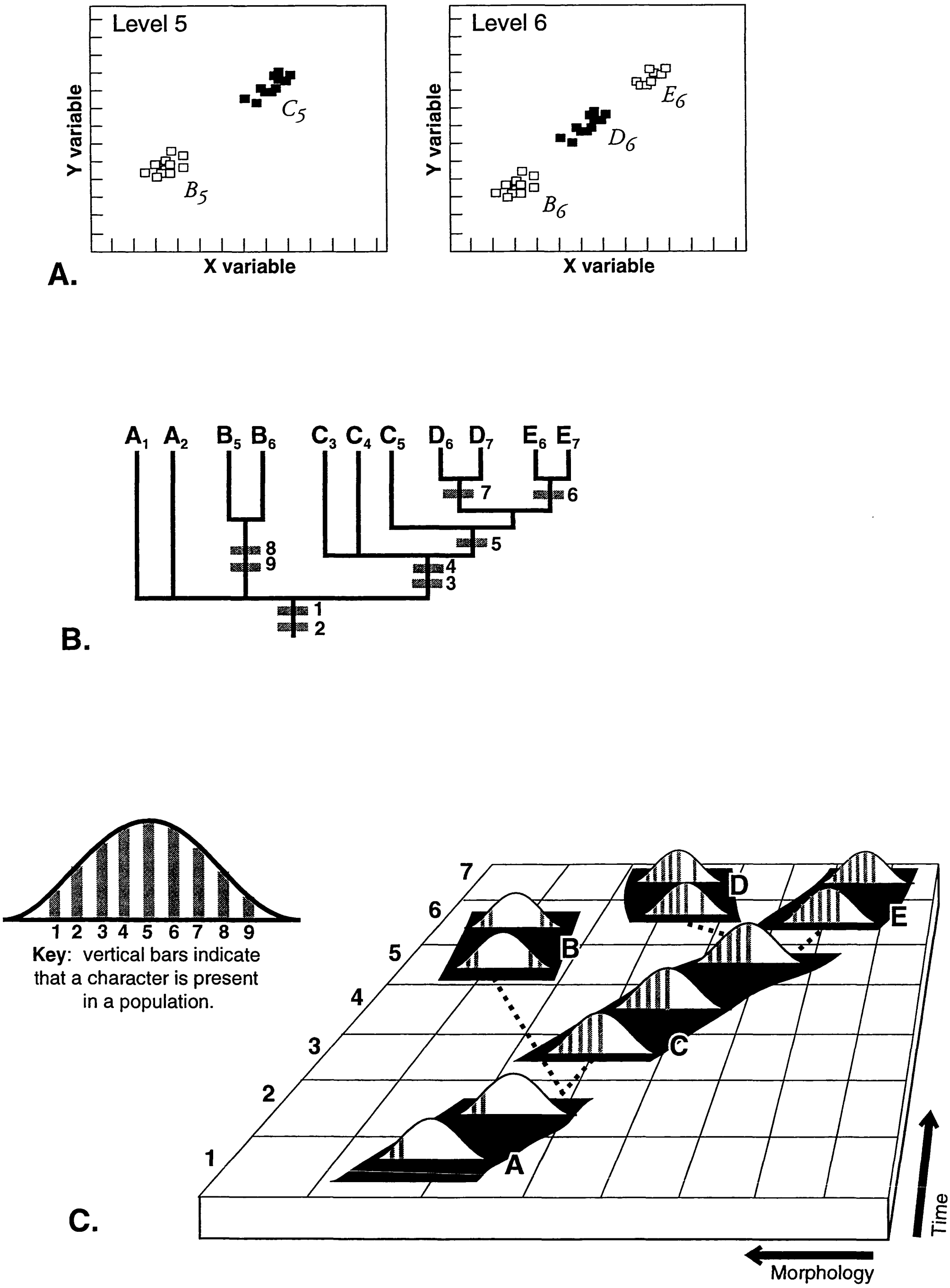


FIG. 3—Summary of steps in stratocladistic analysis. A, Operational Phylogenetic Units (OPUs) are chosen by using multivariate discrimination techniques on fossil samples from a single time horizon. B, cladistic analysis based on discrete morphological characters produces a most-parsimonious cladogram. C, a combination of morphologic and stratigraphic data produces a phylogenetic tree with minimal total parsimony debt. Species-level taxa can be delimited on this tree after the analysis is complete. See text for a detailed discussion and explanation.

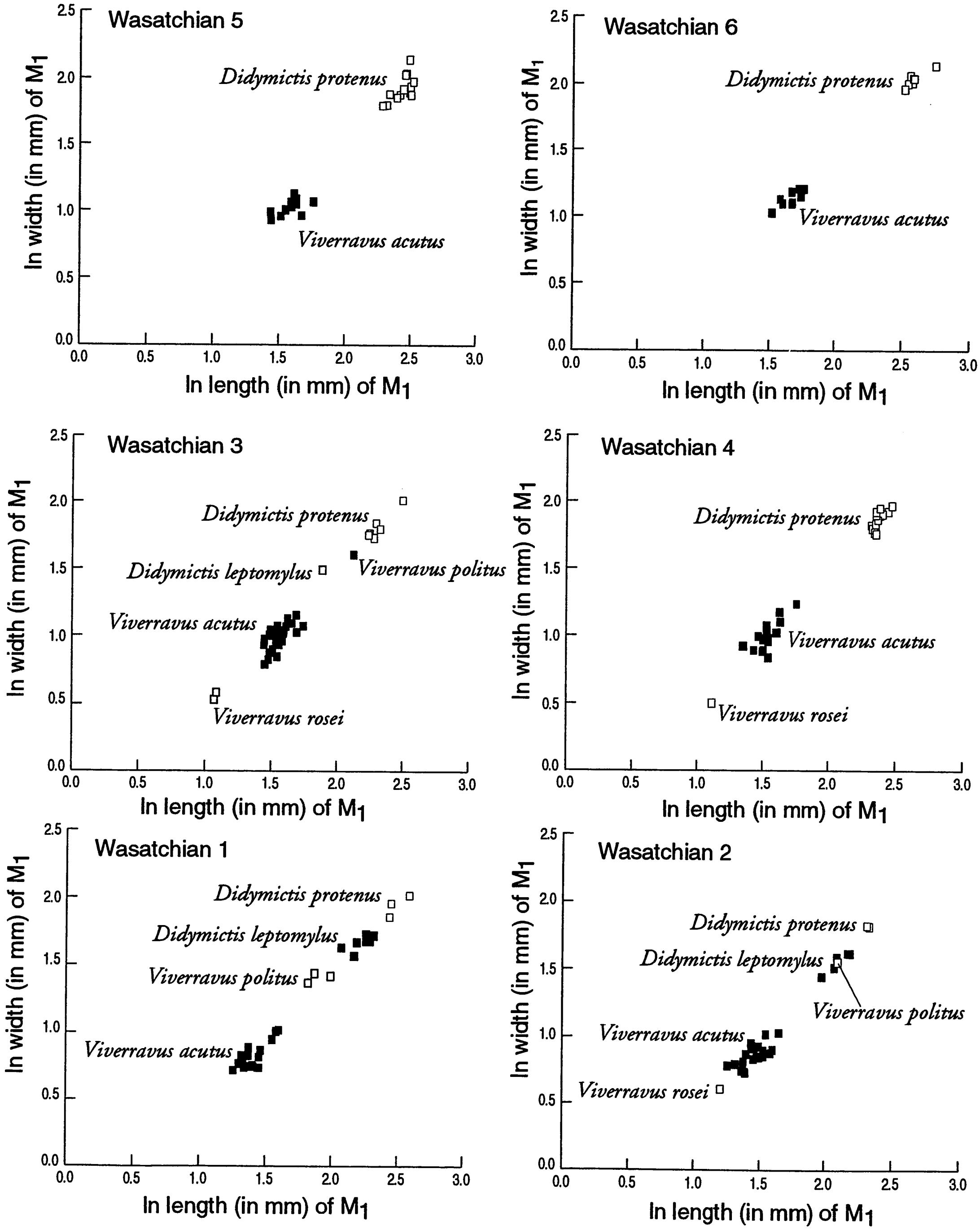


FIG. 4—Number of Operational Phylogenetic Units (OPUs) present in each faunal zone. This was determined by identifying morphologically discrete clusters. Data from P4, M1, and M2 were considered, although only data from M_1 are presented in this figure. Clusters are labeled *a posteriori* using the species names assigned to them at the end of the analysis. Discussion and summary statistics for each cluster are provided in the text.

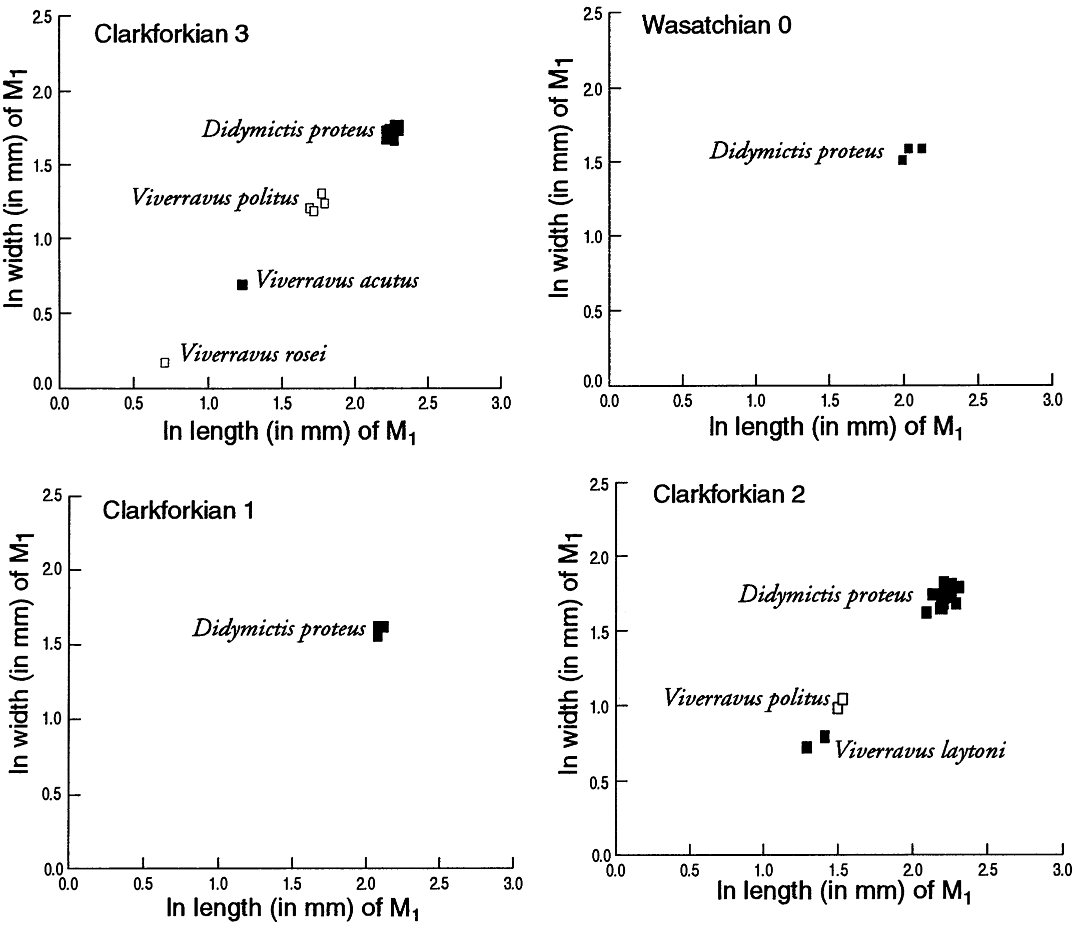


FIG. 4—Continued (caption on facing page).

branching lineages and that there were not nine contemporaneous species, as might be interpreted from the consensus cladogram (Fig. 6A).

Didymictis provides a starkly different example. The relationships among all of the *Didymictis* OPUs were completely resolved in each of the 1470 cladograms (Fig. 6A). These too were parts of long lineages (Figs. 6B, 8), but—unlike *Viverravus*—there was a great deal of anagenetic evolution that resulted in numerous meristic differences between earlier and later members of the group. This was enough to allow a cladistic analysis to resolve their relationships. Even in this case, however, the further resolution provided by stratigraphic data has an important tale to tell. From the cladogram, it is impossible to determine whether the *Didymictis* OPUs were all part of a single unbranched lineage or whether there were as many as eight speciation events. The stratigraphic data allow only a single interpretation from these data—there was a single lineage in the Clarkforkian that split into two at the beginning of the Wasatchian (Fig. 8). It is only through the use of a phylogenetic method that can distinguish ancestor-descendant relationships from true sister-group relationships that these patterns are interpretable.

Discussion.—Flynn and Galiano (1982) argued that members of the genus *Didymictis* are more closely related to *Protictis* than either is to *Viverravus*. They argued that *Protictis haydenianus*, *Bryanictis vanvaleni*, *Bryanictis microlestes*, and *Didymictis* species form a mono-

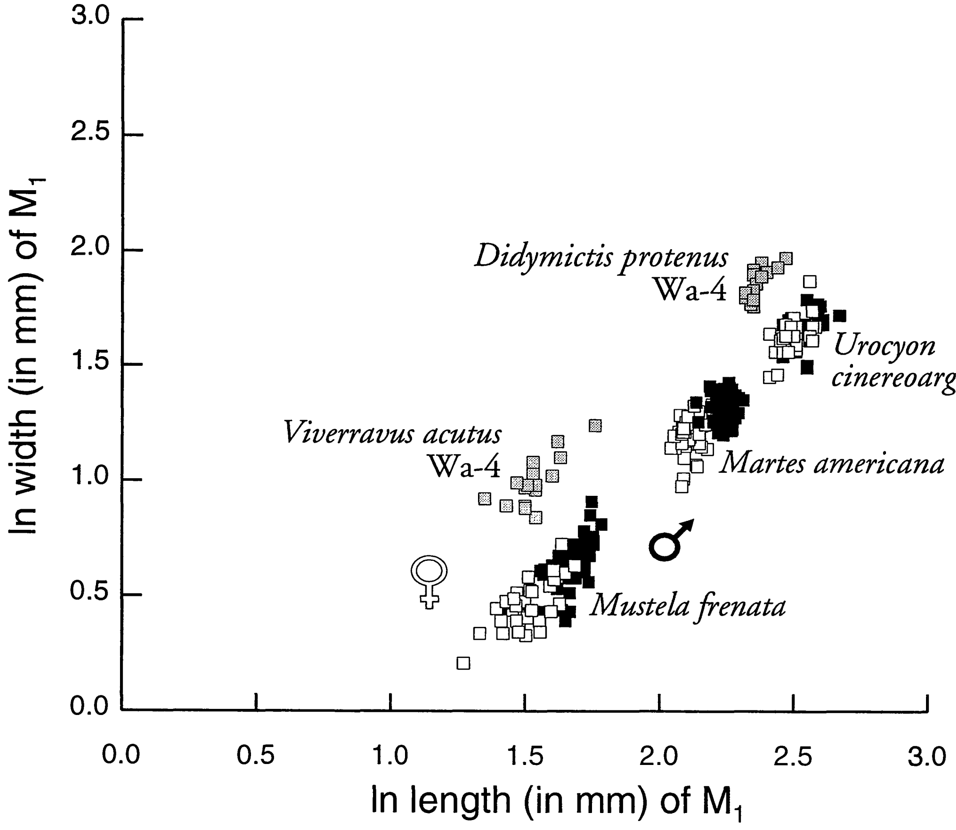
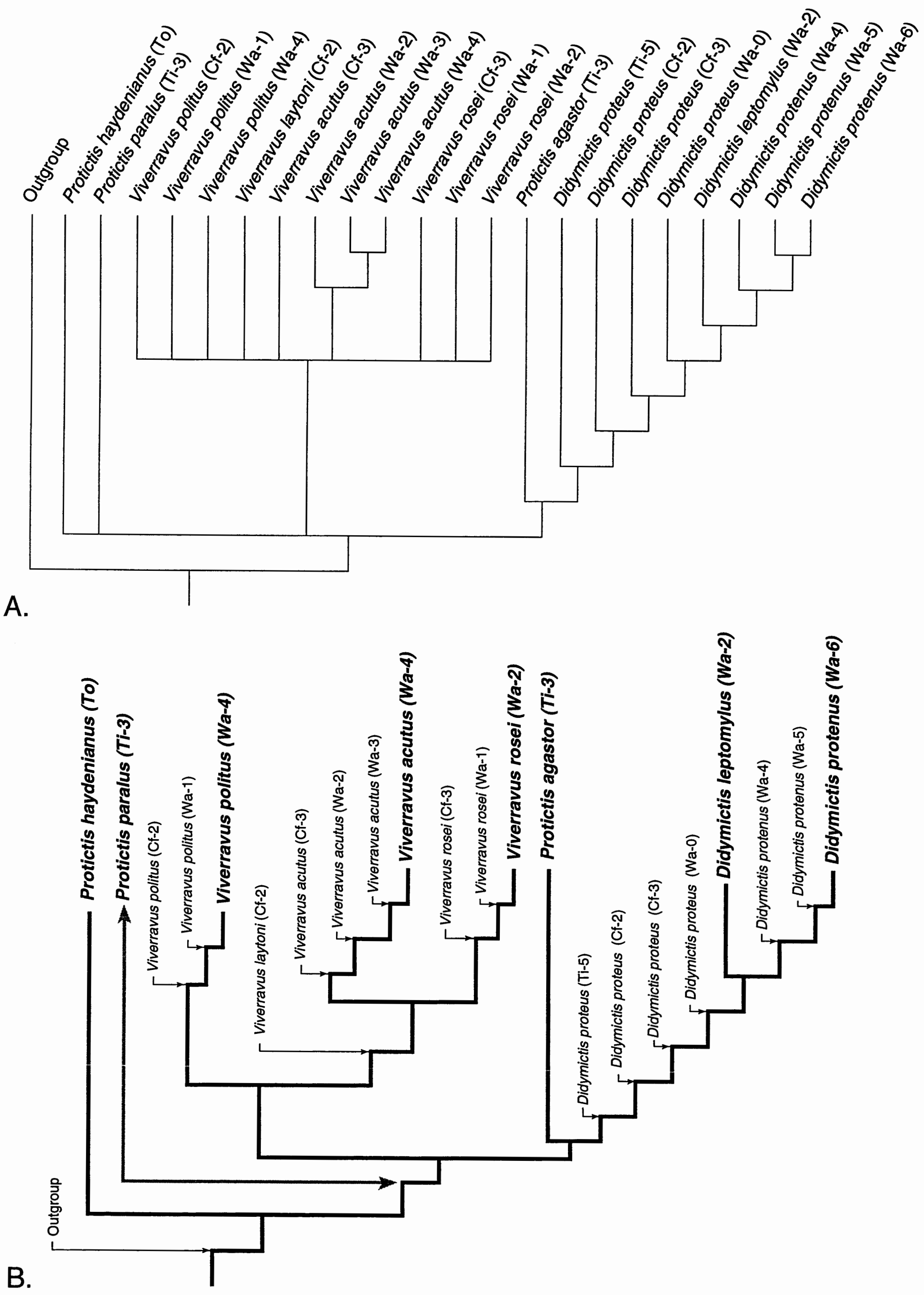


FIG. 5—Clusters of morphologically discrete fossil specimens show size variability similar to those of extant species of carnivorans. *Didymictis*, here represented by *D. protenus* from Wa-4, has a range of variation most similar to that of non-sexually dimorphic species such as foxes (e.g., gray fox *Urocyon cinereoargenteus*). *Viverravus*, here represented by *V. acutus* from Wa-4, has a range of variation more similar to that of sexually dimorphic mustelids (e.g., long-tailed weasel *Mustela frenata* and American martin *Martes americana*). The graph shows natural logs of the lengths and widths of M_1. Fossil individuals of unknown sex are represented by gray squares. For extant species, male individuals are represented by solid squares while females are represented by open squares.

phyletic clade that they named Didymictida. Analysis here indicates that *Didymictis* and *Viverravus* are more closely related to one another than either is to *Protictis haydenianus* (Fig. 6A,B). Because of this, Didymictida is abandoned and the older name Viverravidae is used for all three genera. Other taxa considered by Flynn and Galiano (1982) were not included in the present study; therefore, I am unable to confirm or refute many of their other hypotheses.

FIG. 6 (facing page)—A, strict consensus of 1470 morphologically most parsimonious cladograms. Each of the fundamental cladograms from which the consensus was drawn had a tree length of 74, a consistency index of 0.784, and a retention index of 0.914. B, phylogenetic trees with the smallest total parsimony debt. Terminal taxa are shown in bold type with heavy lines, while ancestral taxa are shown in light type with arrows pointing to their correct position on the tree. *Protictis paralus* is equivocal in its placement as a terminal taxon or at an ancestral node.


A.
Outgroup
Protictis haydenianus (To)
Protictis paralus (Ti-3)
Viverravus politus (Cf-2)
Viverravus politus (Wa-1)
Viverravus politus (Wa-4)
Viverravus laytoni (Cf-2)
Viverravus acutus (Cf-3)
Viverravus acutus (Wa-2)
Viverravus acutus (Wa-3)
Viverravus acutus (Wa-4)
Viverravus rosei (Cf-3)
Viverravus rosei (Wa-1)
Viverravus rosei (Wa-2)
Protictis agastor (Ti-3)
Didymictis proteus (Ti-5)
Didymictis proteus (Cf-2)
Didymictis proteus (Cf-3)
Didymictis proteus (Wa-0)
Didymictis leptomylus (Wa-2)
Didymictis protenus (Wa-4)
Didymictis protenus (Wa-5)
Didymictis protenus (Wa-6)
B.
Outgroup
Protictis haydenianus (To)
Protictis paralus (Ti-3)
Viverravus politus (Cf-2)
Viverravus politus (Wa-1)
Viverravus politus (Wa-4)
Viverravus laytoni (Cf-2)
Viverravus acutus (Cf-3)
Viverravus acutus (Wa-2)
Viverravus acutus (Wa-3)
Viverravus acutus (Wa-4)
Viverravus rosei (Cf-3)
Viverravus rosei (Wa-1)
Viverravus rosei (Wa-2)
Protictis agastor (Ti-3)
Didymictis proteus (Ti-5)
Didymictis proteus (Cf-2)
Didymictis proteus (Cf-3)
Didymictis proteus (Wa-0)
Didymictis leptomylus (Wa-2)
Didymictis protenus (Wa-4)
Didymictis protenus (Wa-5)
Didymictis protenus (Wa-6)

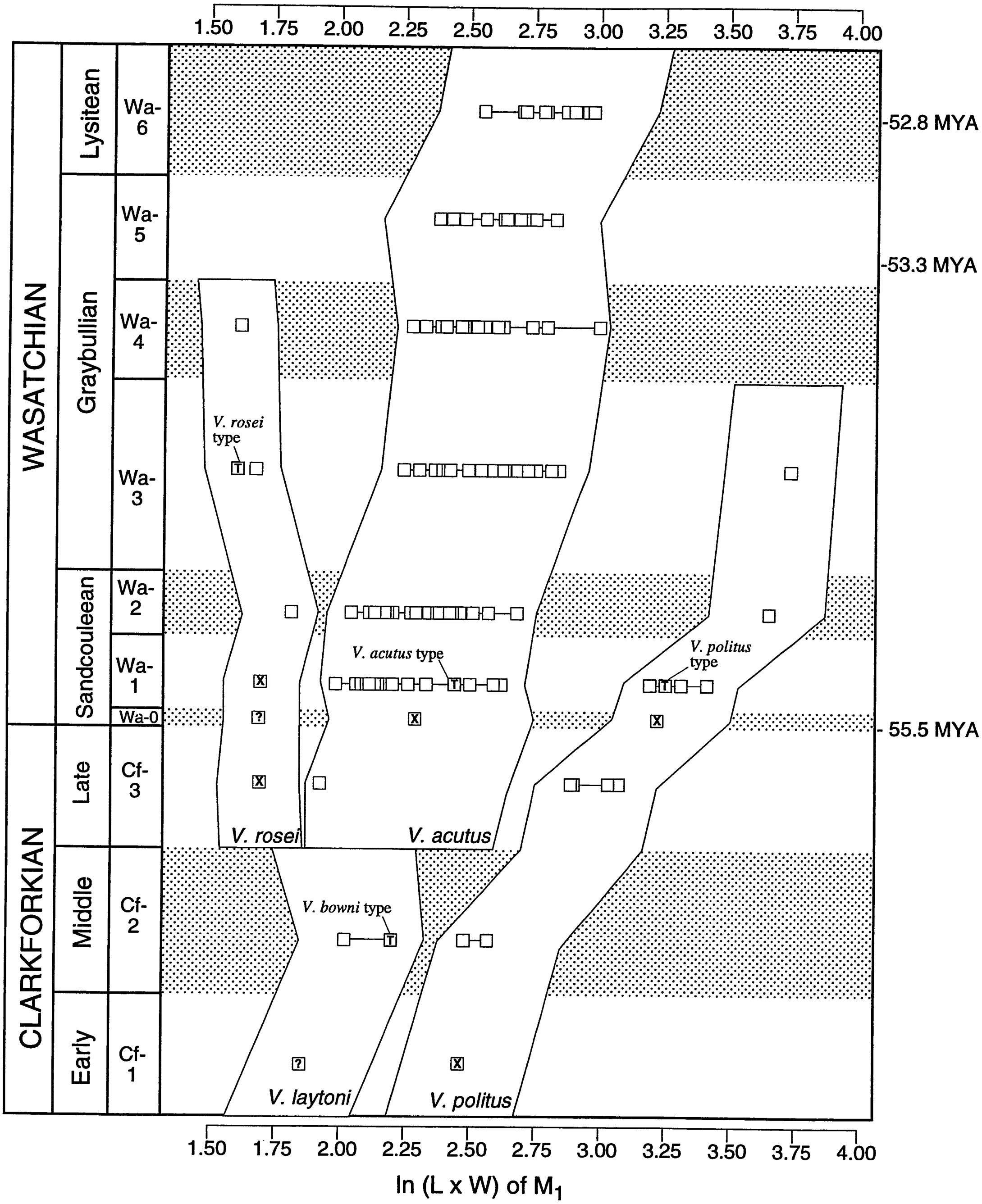


FIG. 7—Phylogenetic tree showing the relationships of species of *Viverravus* from the Clarkforkian and Wasatchian. The topology is derived from the tree in Figure 6B. Individual specimens from each faunal zone are plotted according to the natural log of length multiplied by width of their M_1 to facilitate comparison with Figure 4. **T** = type specimen. **X** = taxon present, but no M_1 data are available. **?** = taxon unknown from interval. White boxes delimit evolutionary species—they do not represent measurements of variability nor rates of evolution.

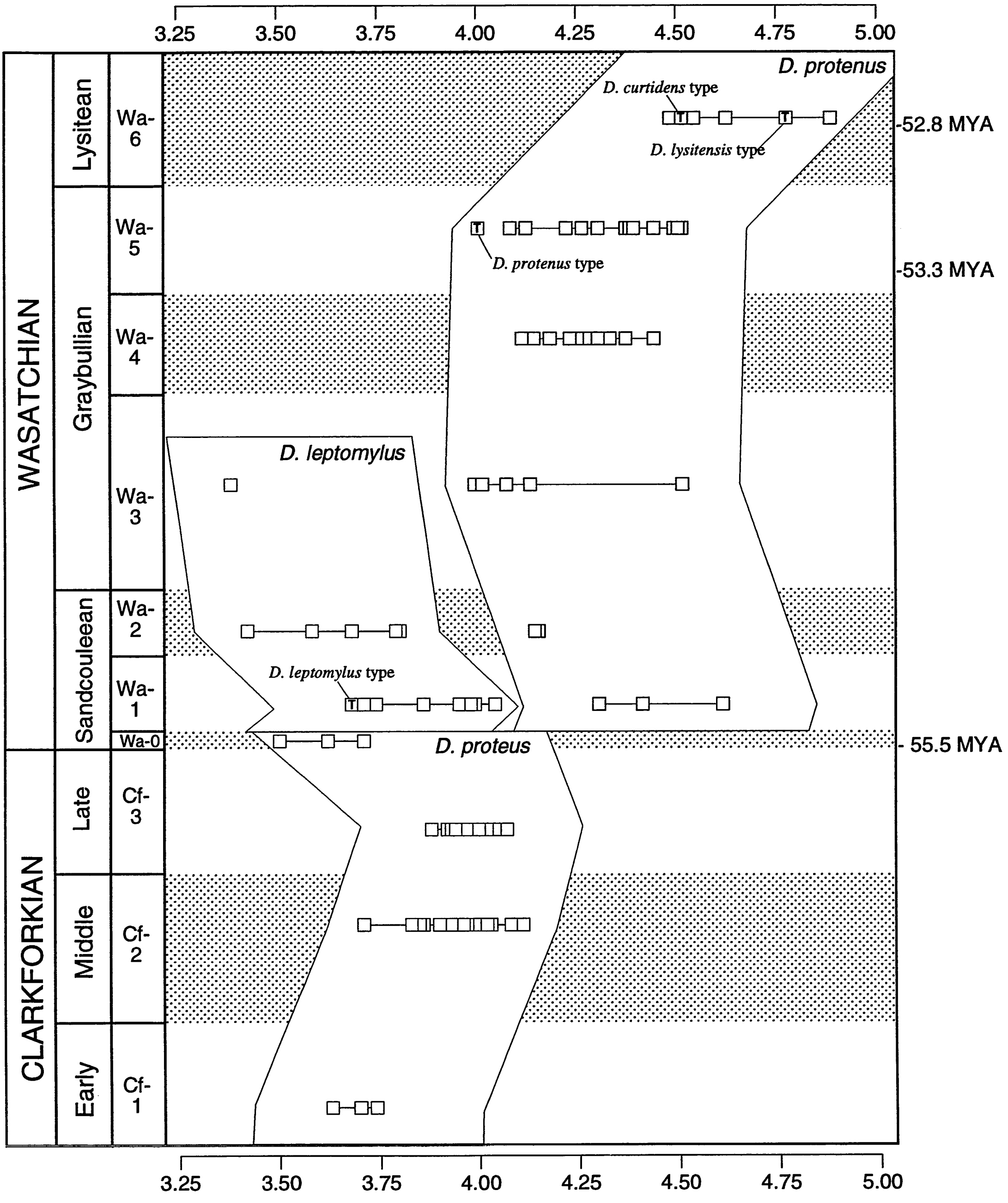


FIG. 8—Phylogenetic tree showing the relationships of species of *Didymictis* from the Clarkforkian and Wasatchian. The topology is derived from the tree in Figure 6B. Individual specimens from each faunal zone are plotted according to the natural log of the length times the width of their M_1 to facilitate comparison with data presented in Figure 4. **T** = type specimen. **X** = taxon present, but no M_1 data are available. **?** = taxon unknown from interval. The white boxes delimit evolutionary species—they do not represent measurements of variability nor rates of evolution.

Gingerich and Winkler (1985) hypothesized that the Tiffanian species *Protictis dellensis* and *Protictis schaffi* were ancestral to Clarkforkian and Wasatchian *Didymictis* and *Viverravus* respectively. This is partially confirmed. *Protictis dellensis* (*sensu* Gingerich and Winkler, 1985) does appear to be ancestral to *Didymictis* and is considered here to be the earliest part of the evolutionary species *Didymictis proteus*. *Protictis schaffi* appears to be an early part of the unbranched lineage containing *Viverravus politus*, but is not ancestral to other species of *Viverravus*. *Protictis laytoni* (*sensu* Gingerich and Winkler, 1985), however, is ancestral to the other species of *Viverravus* and seems to be an early segment of a single unbranched lineage containing the material referred to *Viverravus bowni* (Fig. 7). This makes the genus *Viverravus* polyphyletic with respect to *Protictis*. *P. laytoni* is, therefore, moved to the genus *Viverravus* and *P. schaffi* is placed in the species *V. politus*.

ABBREVIATIONS

AMNH — American Museum of Natural History, New York
UM — Museum of Paleontology, University of Michigan, Ann Arbor

SYSTEMATIC PALEONTOLOGY

Order CARNIVORA
Family VIVERRAVIDAE

Type genus.—Viverravus, Marsh, 1872.

Included genera.—Bryanictis MacIntyre, 1966 [Torrejonian]; *Didymictis* Cope, 1875 [Tiffanian through Bridgerian]; *Ictidopappus* Simpson, 1935 [Torrejonian]; *Intyrictis* Gingerich and Winkler, 1985 [Torrejonian]; *Pappictidops* Qiu and Li, 1977 [late Paleocene and earliest Eocene]; *Pristinictis*, Fox and Youzwyshyn, 1994 [Tiffanian]; *Protictis* Matthew, 1937 [Torrejonian and Tiffanian]; *Protictoides* Flynn and Galiano, 1982 [Uintan]; *Raphictis* Gingerich and Winkler, 1985 [Tiffanian]; *Simpsonictis* MacIntyre, 1962 [Torrejonian]; and *Viverravus* Marsh, 1872 [Tiffanian through Uintan].

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

Viverravus Marsh, 1872

Viverravus Marsh, 1872, p. 127.
Protictis (in part), Gingerich and Winkler, 1985, p. 103.

Type species.—Viverravus gracilis, Marsh, 1872, p. 127.

Included species.—Viverravus acutus, Matthew and Granger, 1915; *V. gracilis*, Marsh, 1872; *V. laytoni* (Gingerich and Winkler, 1985); *V. lutosus*, Gazin, 1952; *V. minutus*, Wortman, 1901; *V. politus*, Matthew and Granger, 1915; *V. rosei* new species; *V. sicarius*, Matthew, 1909.

Viverravus laytoni (Gingerich and Winkler, 1985)

Viverravus acutus, Rose, 1981, p. 100, in part.
Viverravus, undescribed new species, Rose, 1981, p. 101, in part.
Viverravinae sp. A, Rose, 1981, p. 156.

Protictis laytoni Gingerich and Winkler, 1985, p. 107, fig. 9.
Viverravus bowni Gingerich, 1987, p. 312, fig. 24.

Holotype.—PU 16523.

Type locality.—Princeton Quarry, Fort Union Formation, Clarks Fork Basin, Wyoming.

Age and distribution.—Late Tiffanian through middle Clarkforkian (late Paleocene) of Wyoming.

Definition.—An evolutionary species consisting of the series of ancestor-descendant populations between speciation (cladogenic) events that contains the holotype of *Viverravus laytoni* (PU 16523).

Diagnosis.—Differs from *Viverravus politus* and *V. acutus* in being somewhat smaller, differs from *V. rosei* in being larger, and further differs from *V. politus* in having a proportionally larger P_3 and a proportionally smaller protoconid on the lower molars.

Referred specimens.—**Middle Clarkforkian** [Cf-2]: **SC-29**: UM 76928 [holotype of *V. bowni*], 76929, and 76930. **SC-117**: UM 73654. **SC-188**: UM 71578 and 71579. **SC-197**: UM 71577.

Description.—The lower canine of this species is relatively long and smooth-surfaced. There is a cristid running from its tip to its posterior base. P_2 is a two-rooted tooth with a tiny posterior accessory cusp. The main cusp of the tooth is positioned over its anterior root. P_3 is also double-rooted, but the main cusp is positioned approximately in the middle of the anteroposterior axis. There are two posterior accessory cusps on this tooth, the first of which is conical and positioned relatively high on the posterior margin of the main cusp. There is also a tiny anterior accessory cusp. P_4 is a little longer than P_3 and a little higher-cusped. It has a small anterior accessory cusp, an extremely high main cusp, a large first posterior accessory cusp, which is positioned high on the posterior margin of the main cusp, and a small second posterior accessory cusp. There is a small notch between the main cusp and the first posterior accessory cusp, but not between any of the other cusps. There are light basal cingulids along the labial crown above the roots, but they are not connected to one another.

M_1 has a very tall protoconid. The paraconid and metaconid are subequal in height and the latter is positioned lingual to the posterior face of the protoconid. There are three, relatively tall talonid cusps, a hypoconid, hypoconulid, and entoconid. The talonid basin is deep, sloping dramatically from its high point near the hypoconulid to its low point at the talonid notch. There are light proto- and basal cingulids along the labial side of the talonid. The hypoflexid is not rimmed by a cingulid. M_2 is much smaller than M_1 and the trigonid cusps are somewhat taller than the talonid. The talonid is slightly longer anteroposteriorly than the trigonid, and the former is much narrower than the latter. The protoconid is the tallest trigonid cusp and the paraconid is the lowest. The latter is positioned fairly far anteriorly. The hypoconulid is the tallest talonid cusp and the hypoconid and entoconid are relatively indistinct. The talonid basin dips deeply at the talonid notch.

Measurements of the posterior cheek teeth of Clarkforkian *Viverravus laytoni* are presented in Table 2.

Discussion.—This species was originally described as *Protictis laytoni* by Gingerich and Winkler (1985). This study indicates that this species is part of a single, unbranched lineage with which also contains *Viverravus bowni* (Gingerich, 1987). These two species are here synonymized and placed within the genus *Viverravus*. The material referred here to *V. laytoni* contains some of that referred to *Viverravus acutus* and an undescribed new species by Rose (1981). The specimens he reported from the *Plesiadapis cookei* and *P. gingerichi* zones (Cf-2 and Cf-1 respectively) are referred here to *Viverravus laytoni*. Those from the *Phenacodus-Ectocion* Zone (Cf-3) are referred here to *V. acutus*.

TABLE 2—Summary of measurements of the lower cheek teeth of *Viverravus laytoni* from the Clarks Fork Basin, Wyoming. Specimens included here are from the middle Clarkforkian (Cf-2). All measurements in millimeters.

Tooth position	N	Observed range	Mean	Standard deviation	Coefficient of variation
Lower dentition					
P_4 L	1	3.40	—	—	—
W	1	1.46	—	—	—
M_1 L	3	3.65 - 4.10	3.81	0.2542	6.68
W	2	2.06 - 2.20	2.13	—	—
M_2 L	2	2.60 - 2.63	2.62	—	—
W	2	1.50 - 1.60	1.55	—	—

Viverravus acutus Matthew and Granger, 1915
Fig. 9

Viverravus acutus Matthew and Granger, 1915, p. 27, figs. 20 and 21. McKenna, 1960, p. 95.
Viverravus cf. *V. acutus*, Bown, 1979, p. 94.
Viverravus acutus (in part), Rose, 1981, p. 100.
Viverravus undescribed new species (in part), Rose, 1981, p. 101.
Didymictidae genus and species indeterminate, Davidson, 1987, p. 120.
Viverravus bowni (in part), Gingerich, 1989, p. 37.

Holotype.—AMNH 16112.

Type locality.—According to Matthew and Granger (1915) the type specimen is from the "intermediate beds, 3 mi. SE of the mouth of Pat O'Hara Creek," Sand Coulee beds, early Eocene. University of Michigan field work indicates that this area is mostly from beds assigned a Wa-1 age (Gingerich, pers. comm.).

Age and distribution.—Late Clarkforkian (Cf-3) through late Wasatchian (Wa-6) of North America.

Definition.—An evolutionary species consisting of the series of ancestor-descendant populations occurring between speciation (cladogenic) events that contains the type specimen of *Viverravus acutus* (AMNH 16112).

Diagnosis.—Differs from *Viverravus rosei* and *V. laytoni* in being somewhat larger, differs from *V. politus* in being smaller and in having a relatively larger P_3 and shorter protoconid on M_1.

Referred specimens.—**Late Clarkforkian** [Cf-3]: **SC-10**: UM 64713. **SC-347**: UM 83797. **Early Sandcouleean** [Wa-0]: **SC-67**: UM 87339. **Middle Sandcouleean** [Wa-1]: **FG-18**: UM 75840 and 75908. **SC-1**: UM 75977, 81975, and 83210. **SC-4**: UM 83081 and 98222. **SC-7**: UM 64704 and 83087. **SC-26**: UM 74043. **SC-38**: UM 63291, 75603, and 75961. **SC-39**: UM 65377. **SC-123**: UM 67065. **SC-161**: UM 68400, 68698, 69870, 77450, 80533, 80546, 86031, and 86125. **SC-210**: UM 72084, 72111, 72141, 81635, and 87428. **SC-287**: UM 73771. **SC-331**: UM 82493. **Late Sandcouleean** [Wa-2]: **MP-23**: UM 87640 and 87672. **MP-219**: UM 95964. **MP-238**: UM 96413. **MP- 243**: UM 96780. **MP-277**: UM 99197. **SC-2**: UM 64542, 64545, 64735, 67479, 76348, and 98170. **SC-31**: UM 65268. **SC-46**: UM 66403 and 97980. **SC-47**: UM 74111 and 86532. **SC-54**: UM 66959 and 76002. **SC-87**: UM 79814 and 82119. **SC-96**: UM 77332. **SC-133**: UM 68046, 68104, 71755, 79681, 79702, 75058, 83515, and 101813. **SC-160**: UM 68130. **SC-207**: UM 69479 and 69512. **SC-300**: UM 75117. **Early Graybullian** [Wa-3]: **MP-138**: UM 93288. **MP-145**: UM 93496 and 93543. **MP-158:** 93895. **MP-174**: UM 94324. **MP-228**: UM 96214. **MP-275**: UM 99176. **SC-32**: UM 78949. **SC-34**: UM 65314 and 94954. **SC-35**: UM 73942, 73965, and 75013. **SC-128**: UM 67036, 76704, and 79171. **SC-192**: UM 68894, 69642, 79222, 79268, 79280, 79318, 81906, 82876, 82891, 82937, 82940, 83211, and 85762. **SC-213**: UM 71070, 71122, 75386, and 79514. **SC-237**: UM 76806. **SC-290**: UM 73822. **SC-312**: UM 76653. **SC-323**: UM 79343. **Middle Graybullian** [Wa-4]:

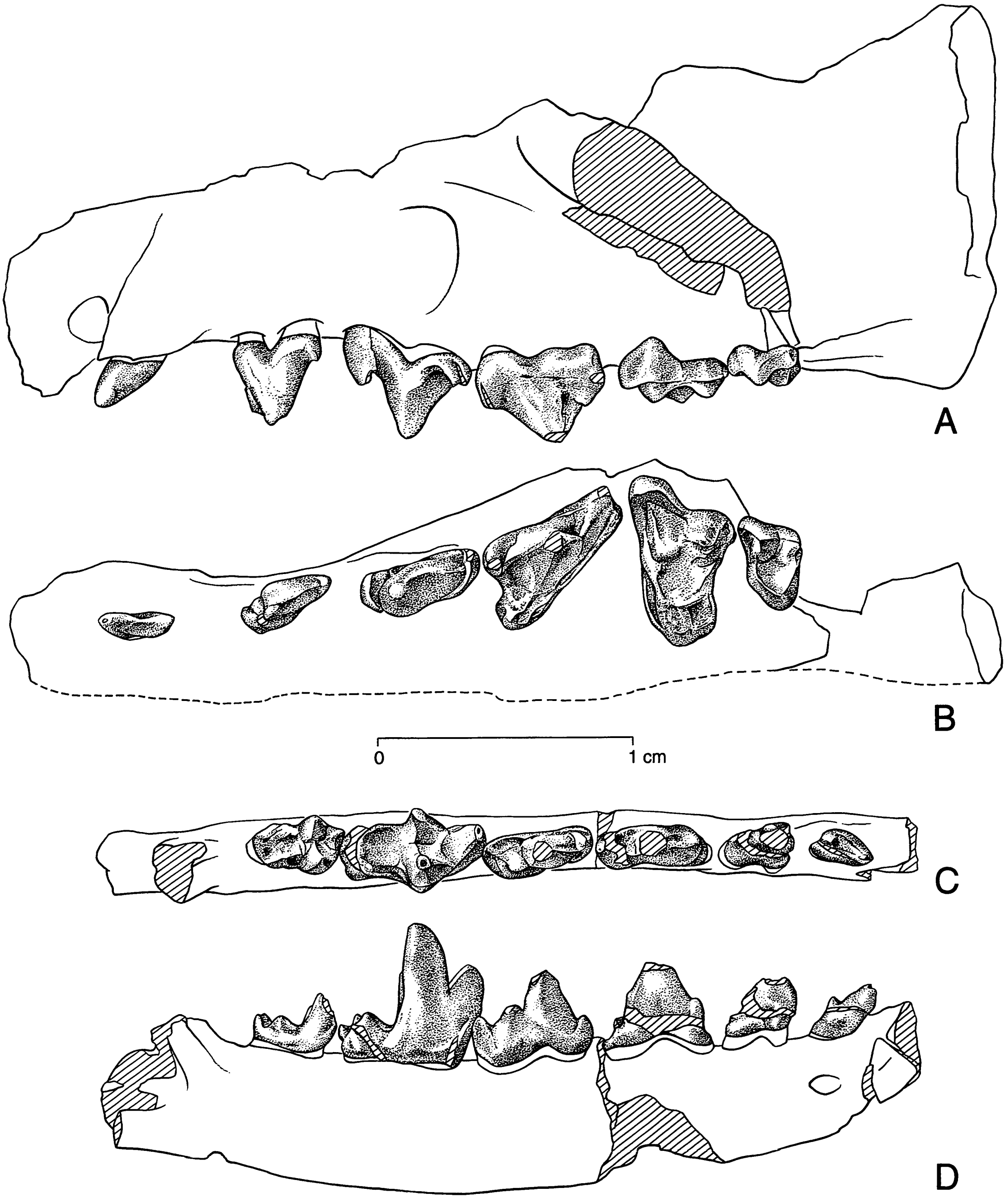


FIG. 9—Upper and lower dentitions of *Viverravus acutus* from the Wasatchian of the Clarks Fork Basin, Wyoming: left maxilla (UM 79171, SC-128) with P^1-M^2 in lateral (A) and occlusal views (B), and right dentary with P_1-M_2 in occlusal (C) and lateral views (D). Some distortion is caused by breakage in P_{1-3} and M_1.

MP-17: UM 87006. **MP-122**: UM 92456 and 92460. **MP-142**: UM 93370. **MP-167**: UM 99334. **MP-175**: UM 94380. **SC-64**: UM 66671. **SC-112**: UM 74062. **SC-113**: UM 73632. **SC-147**: UM 67313. **SC-148**: UM 67326. **SC-253**: UM 74634. **SC-255**: UM 73276, 73200, 73127, 73208, and 73247. **SC-256**: UM 73548. **SC-265**: UM

87708. **SC-325**: UM 79466, 79470, and 79481. **YM-421**: UM 64104. **Late Graybullian** [Wa-5]: **MP-62**: UM 91755 and 91796. **MP-65**: UM 91318, 97092, and 97107. **MP-86**: UM 91948 and 94551. **MP-151**: UM 93712. **MP-152**: UM 93731, 93736, and 95314. **MP- 159**: UM 93976. **MP-173**: UM 95028. **SC-295**: UM 87731. **Lysitean** [Wa-6]: **MP-4**: UM 82413. **MP-41**: UM 88231 and 96736. **MP-42**: UM 88291. **MP-51**: UM 91172. **MP- 73**: UM 91457. **MP-76**: UM 91517. **MP-81**: UM 91630. **MP-83**: UM 91725. **MP-102**: UM 92193. **MP-118**: UM 92381.

Description.—The more than 140 *Viverravus acutus* specimens listed here dramatically increase our knowledge of the morphology and variability of this species. This species exhibits a relatively wide range of variation, comparable to that of sexually dimorphic species of living carnivorans (see "Results" section above). Presumably, individuals in the small size range of any given stratigraphic level represent females of the species, and those in the larger size range represent males. It is impossible, however, to make an accurate identification of the sex of any individual specimen.

The dental formula for the species is $I^3_?\ C^1_1\ P^4_4\ M^2_2$. Most specimens have robust dentaries, although those of some individuals are quite shallow. Mental foramina are found below P_1 and P_3. In specimens in which it is preserved, the masseteric fossa is not as deep as in *Viverravus rosei* or *V. laytoni*. The infraorbital canal is small and fairly circular in outline.

P_1, in specimens in which it is preserved, is small and two-rooted. It has a relatively simple crown with a single cusp. In one specimen (UM 71070) there is a tiny accessory cusp at the posterior border of the crown. P_2, also single-cusped and two-rooted, has a main cusp positioned relatively far forward on the crown such that it is over the posterior portion of the anterior root of the tooth. There are no accessory cusps. P_3 also has an anteriorly positioned main cusp, but this tooth has a tiny anterior accessory cusp and both first and second posterior accessory cusps. There is a small lingual cingulid connecting the second posterior accessory cusp with the base of the main cusp on its medial side. P_4 has a centrally positioned main cusp with accessory cusps that are larger than those on P_3. The anterior accessory cusp is the smallest of these. It projects forward and there is a small notch between it and the base of the main cusp. A small cingulid connects it on the lingual side of the tooth to the base of the main cusp. There are notches between the main cusp and the first posterior accessory cusp and between the latter and the second accessory cusp. As in most *Viverravus* species, a lingual cingulid connects the second posterior accessory cusp with the base of the main cusp forming a small posterior basin. There is some variation in the shape of the crown and the development of labial cingulids on P_4. In larger specimens, the crown is longer and the main cusp forms a more obtuse angle than in smaller specimens, which appear relatively shorter and higher-cusped. The latter morphology, similar to that seen in the type specimens of *Viverravus gracilis* and *V. dawkinsianus*, is more common in the late Sandcouleean and Lysitean specimens. The former morphology is similar to that seen in the type of *Viverravus acutus* and is more common in individuals from lower in the stratigraphic range. These differences are apparently related to the size of the animal (which, in turn, is probably related to the sex of the individual); in horizons from the middle of the stratigraphic range (such as Wa-3) small individuals have the higher-cusped morphology, while large individuals have the lower-cusped morphology. Specimens of intermediate size, have an intermediate morphology. Likewise, larger specimens sometimes have faint labial cingulids developed at the anterior and posterior of the crown base. Smaller specimens show no trace of these cingulids, while intermediate-sized specimens have faintly developed cingulids.

The protoconid of M_1 is by far the tallest of the trigonid cusps; the paraconid and metaconid are subequal in height. The metaconid is not posteriorly positioned and the trigonid does not have an open appearance. There are three well developed cusps around the talonid basin. The hypoconid is the tallest of these and the entoconid the shortest. The hypoconulid is closer to the hypoconid than to the entoconid. The talonid notch is deep and the floor of the talonid basin slopes sharply from its high point between the hypoconid and hypoconulid to its low point at the mouth of the talonid notch. There is no notch in the entocristid above the hypoflexid. In many specimens, there is a cingulid along the labial base of the talonid from the hypoconulid to the base of the protoconid. This is variably developed, however, and is faint in some specimens. A precingulid is present, but indistinct in many specimens. M_2 is considerably smaller than M_1, although the talonid basin is proportionally longer in the former. The metaconid and protoconid are subequal in height and the paraconid is the shortest of the three trigonid cusps. The hypoconid, hypoconulid, and entoconid are all well developed and approximately equally spaced around the posterior rim of the talonid. The talonid notch is not as deep as in the M_1 and the floor of the basin is more level than in the M_1.

No incisors are preserved in any of the specimens of this species, but a partial skull (UM 69870) has alveoli for three upper incisors. They were arranged in a gently curved row, similar to that in canids. A diastema for the lower canine separates I^3 from the upper canine. There is a deep recess in the premaxilla for the reception of the lower canine. No upper canines are preserved, but the alveoli in UM 69870 indicate that they were fairly robust and rounded in cross-section. P^1 is a small, single-cusped, double-rooted tooth. It is separated from the upper canine by an extremely short diastema. The crown consists of a single cusp positioned over the anterior root of the tooth. P^2 is considerably larger than P^1 and more laterally compressed. Its crown consists of a centrally positioned main cusp with the hint of a small posterior accessory cusp. P^3 is laterally compressed with a very small lingual swelling at its base over the posterior root. The tooth is two-rooted with one main cusp and a small posterior cusp. A lingual cingulum runs from the posterior accessory cusp to the posterior base of the main cusp on P^4.

M^1 is triangular in outline with a very large, hooked parastyle and a much smaller metastyle separated by an ectoflexus. There is a small stylar shelf labial to both the paracone and metacone, which is bordered by a low cingulum. The paracone is slightly taller than the metacone and both are significantly taller than the protocone. The preparacone crista extends to the labial edge of the tooth on the parastyle, but does not continue to its anterior point. There is no metaconule, although there is a distinct paraconule with a preparaconule crista that extends labially to the anteriormost point of the parastyle. A precingulum is found low on the anterior base of the protocone, which extends labially towards the base of the paracone. It is not connected to the postcingulum, which is large and positioned high along the posterior base of the protocone. The postcingulum flares posteriorly and often contains a small hypocone. In some specimens, the postcingulum continues labially towards the metastyle, while in others it ends along the posterior border of the crown lingual to the metacone. The former morphology is more common in larger individuals from the upper part of the stratigraphic range of the species. M^2 is much smaller than M^1. Its parastyle is larger than the metastyle, but both are shorter than those on M^1. The metacone is significantly taller than the paracone and the protocone is intermediate in height. No conules are visible in any of the Michigan specimens. In larger, later individuals, there are both pre- and postcingula present, but neither are as well developed as they are on M^1. The stylar shelf is considerably narrower than that of M^1, but it is still bounded labially by a low cingulum.

Measurements of the posterior cheek teeth of Clarkforkian and Wasatchian *Viverravus acutus* are presented in Table 3.

Discussion.—Rose (1981) reported two species of *Viverravus* (*V. acutus* and an undescribed new species) from the Clarkforkian. The specimens he reported from the *Phenacodus-Ectocion* Zone (Cf-3) are referred here to *Viverravus acutus*. Those from the *Plesiadapis cookei* and *P. gingerichi* zones (Cf-2 and Cf-1 respectively) are referred to *V. laytoni*. The *Viverravus acutus* lineage may also include the Lostcabinian *V. lutosus* and the Bridgerian *V. gracilis*, but these horizons are beyond the scope of the current study. If these should prove to belong to the same species lineage as *Viverravus acutus*, then all of the material described here should receive the name *Viverravus gracilis*.

TABLE 3—Summary of measurements of upper and lower cheek teeth of *Viverravus acutus* from the Bighorn and Clarks Fork Basins, Wyoming. Specimens included here are from the late Clarkforkian (Cf-3) through late Wasatchian (Wa-6). Change in the size of this species through time contributes to its overall variability (see Fig. 7). For this reason, statistics are tabulated by faunal zone. All measurements in millimeters.

Tooth position	N	Observed range	Mean	Standard deviation	Coefficient of variation
Cf-3					
Lower dentition					
M_1 L	1	3.42	—	—	—
W	1	2.00	—	—	—
M_2 L	1	2.70	—	—	—
W	1	1.54	—	—	—
Wa-1					
Upper dentition					
P^4 L	4	4.06 - 4.39	4.26	0.1421	3.34
W	4	4.14 - 4.39	4.46	0.3665	8.22
M^1 L	4	2.66 - 3.17	2.97	0.2208	7.43
W	4	4.16 - 5.05	4.56	0.3747	8.22
M^2 L	3	1.68 - 1.73	1.70	—	—
W	3	2.99 - 3.54	3.17	—	—
Lower dentition					
P_4 L	8	3.08 - 3.65	3.42	0.2058	6.02
W	8	1.15 - 1.52	1.35	0.1222	9.07
M_1 L	18	3.54 - 4.94	4.10	0.3991	9.73
W	18	2.05 - 2.77	2.28	0.2261	9.93
M_2 L	10	2.46 - 3.10	2.88	0.1952	6.78
W	10	1.29 - 1.71	1.56	0.1092	6.99
Wa-2					
Upper dentition					
M^1 L	1	3.66	—	—	—
W	1	3.66	—	—	—
Lower dentition					
P_4 L	12	3.17 - 4.55	3.80	0.3834	10.09
W	12	1.37 - 1.97	1.59	0.1673	10.53
M_1 L	24	3.51 - 5.20	4.27	0.4128	9.67
W	25	2.08 - 2.80	2.38	0.1912	8.04
M_2 L	5	2.55 - 3.43	3.03	0.3154	10.41
W	5	1.64 - 2.03	1.84	0.1550	8.43
Wa-3					
Upper dentition					
P^4 L	3	3.64 - 4.41	4.11	—	—
W	3	4.55 - 5.66	5.06	—	—
M^1 L	3	3.30 - 4.19	3.79	—	—
W	3	4.78 - 5.79	5.13	—	—
M^2 L	1	2.13	—	—	—
W	1	3.21	—	—	—
Lower dentition					
P_4 L	13	3.46 - 4.80	4.12	0.4056	9.84
W	13	1.38 - 2.02	1.69	0.2006	11.87
M_1 L	27	4.25 - 5.70	4.75	0.3774	7.95
W	27	2.20 - 3.17	2.71	0.2360	8.71
M_2 L	8	2.44 - 3.52	3.18	0.3695	11.61
W	7	1.62 - 2.31	1.93	0.2180	11.32

			Wa-4		
Upper dentition					
P^4 L	2	4.64 - 4.89	—	—	—
W	2	4.40 - 4.98	—	—	—
M^1 L	3	3.33 - 3.48	3.40	—	—
W	3	4.73 - 5.65	5.20	—	—
M^2 L	3	1.95 - 2.27	2.16	—	—
W	3	2.76 - 3.75	3.37	—	—
Lower dentition					
P_4 L	5	3.90 - 5.15	4.55	0.4977	10.93
W	5	1.41 - 1.99	1.68	0.2406	14.34
M_1 L	19	3.85 - 5.79	4.63	0.4037	8.72
W	18	2.31 - 3.44	2.72	0.2881	10.59
M_2 L	4	2.99 - 4.19	3.65	0.4946	13.57
W	4	1.82 - 2.41	2.05	0.2549	12.46
			Wa-5		
Lower dentition					
P_4 L	2	4.38 - 4.72	4.55	0.2404	5.28
W	2	1.67 - 1.95	1.81	0.1980	10.94
M_1 L	12	4.20 - 5.81	4.91	0.4525	9.22
W	12	2.53 - 3.07	2.80	0.1688	6.04
M_2 L	3	3.51 - 3.81	3.64	—	—
W	3	1.94 - 1.98	1.96	—	—
			Wa-6		
Upper dentition					
P^4 L	1	5.32	—	—	—
W	1	6.50	—	—	—
M^1 L	1	3.80	—	—	—
W	1	5.84	—	—	—
M^2 L	1	2.44	—	—	—
W	1	4.10	—	—	—
Lower dentition					
P_4 L	6	4.53 - 5.28	4.95	0.3233	6.54
W	6	1.75 - 2.10	1.95	0.1392	7.13
M_1 L	9	4.57 - 5.87	5.32	0.4374	8.22
W	9	2.77 - 3.31	3.08	0.1800	5.84
M_2 L	3	3.75 - 4.28	3.97	—	—
W	3	2.13 - 2.25	2.18	—	—
			All faunal zones		
Upper dentition					
P^4 L	10	3.64 - 5.32	4.42	0.4562	10.32
W	10	4.14 - 6.50	4.89	0.7225	14.77
M^1 L	12	2.66 - 4.19	3.41	0.42520	12.48
W	12	4.16 - 5.84	5.04	0.5476	10.87
M^2 L	8	1.68 - 2.44	2.02	0.2970	14.72
W	8	2.76 - 4.10	3.37	0.4544	13.49
Lower dentition					
P_4 L	46	3.08 - 5.28	4.09	0.5959	14.58
W	46	1.15 - 2.10	1.64	0.2433	14.82
M_1 L	110	3.42 - 5.87	4.57	0.5406	11.83
W	110	2.00 - 3.44	2.60	0.3290	12.66
M_2 L	34	2.44 - 4.28	3.22	0.4667	14.49
W	33	1.29 - 2.41	1.83	0.2599	14.19

Viverravus rosei, new species

Fig. 10

Holotype.—UM 69960, left mandibular fragment with a broken P_4 and M_1.

Type locality.—University of Michigan locality SC-128 in the Clarks Fork Basin: NW¼, Section 30, T56N, R102W, Park County Wyoming. The type locality is from the early Graybullian (Wa-3) subage of the Wasatchian.

Age and distribution.—Late Clarkforkian (Cf-3) land-mammal age through middle Graybullian (Wa-4) subage of the Wasatchian land-mammal age, early part of the early Eocene.

Definition.—An evolutionary species consisting of the series of ancestor-descendant populations between speciation (cladogenic) events that contains the holotype of *V. rosei* (UM 69960).

Diagnosis.—Differs from *Viverravus laytoni*, *V. acutus*, and *V. politus* in being significantly smaller in all linear dimensions, making it the smallest species of the genus. Further differs, along with *V. laytoni* and *V. acutus*, from *V. politus* in having a more closed trigonid on the lower molars.

Etymology.—Named for Dr. Kenneth Rose, who collected the type specimen and who has contributed greatly to our knowledge of viverravids and the faunas from which they come.

Referred specimens.—**Late Clarkforkian** [Cf-3]: **HG-2**: UM 92284. **Middle Sandcouleean** [Wa-1]: **FG-18**: UM 99228. **SC-182**: UM 68762. **SC-210**: UM 72587. **Late Sandcouleean** [Wa-2]: **SC-2**: UM 82213. **SC-133**: UM 79761 and 83518. **SC-212**: UM 69758. **Early Graybullian** [Wa-3]: **SC-128**: UM 69960 (holotype). **SC-192**: UM 79337. **Middle Graybullian** [Wa-4]: **MP-17**: UM 87020. **MP-186**: UM 94695.

Description.—This species is primarily known from its P_4 and M_1; however a partial skull and some associated post-cranial material (UM 92284) provide more information about the species. The anterior dentition remains completely unknown. P^3_3-M^2_2 are preserved in UM 92284, but the specimen is still partially embedded in a nodule, making it difficult to see the crowns of all of the teeth. The dentary is shallow below the molars, but the coronoid process is tall with a deep masseteric fossa. A circular infraorbital canal opens on the face of the maxilla above P^3.

P_3 has a small anterior accessory cusp and a main cusp positioned almost directly over the anterior root of the tooth. First and second posterior accessory cusps are well developed. The crown of the tooth is tall without lingual or labial cingulids. P_4 is relatively longer and lower crowned. The main cusp is just anterior to the midpoint of the length of the tooth. A small anterior accessory cusp and both first and second posterior accessory cusps are present. There are both lingual and labial cingulids at the posterior end of the tooth. These originate at the tip of the second posterior accessory cusp and travel forward to the lateral sides of the base of the main cusp. The lingual cingulid forms a small basin at the posterior end of the tooth, bounded laterally by the first posterior accessory cusp, anteriorly by the base of the main cusp, and posteriorly by the second posterior accessory cusp. The basin is open lingually.

The M_1 is high cusped, with a small but deep talonid basin. The entoconid, hypoconulid, and hypoconid are all tall and distinct. The hypoconid and hypoconulid are closely approximated at the posterolateral corner of the basin. The floor of the basin is highest at the base of these two cusps and drops toward the anteromedial corner of the basin at the talonid notch. This makes the floor of the talonid basin much more steeply sloped than in other species of *Viverravus*. The anterior end of the cristid obliqua begins at the posterior base of the protoconid and dips slightly before rising to the apex of the hypoconid. The hypoflexid, located lateral to the cristid obliqua, is not bounded at its base by a cingulid. The entocristid, along its path anterior from the entoconid, curves dramatically downward toward the base of the tooth, but rises again anteriorly before it ends against the posterior face of the trigonid.

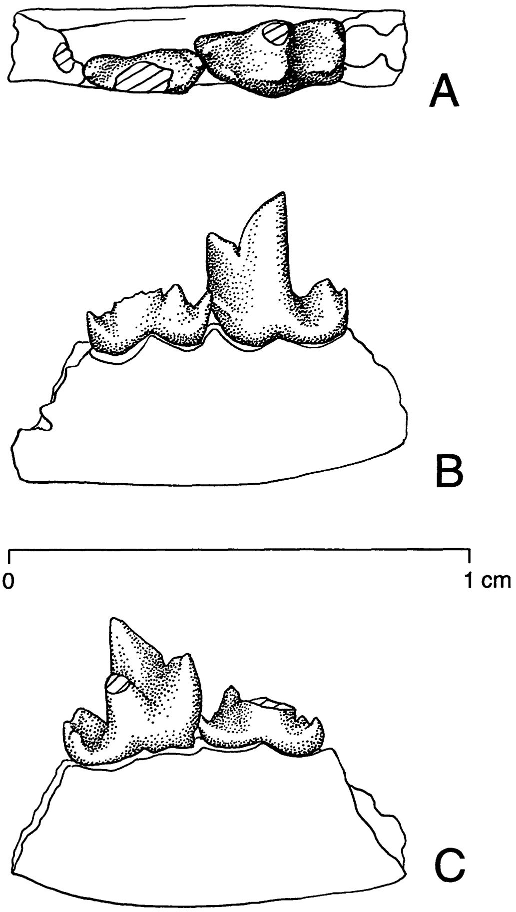


FIG. 10—Lower dentition of *Viverravus rosei* (UM 69960, holotype) from SC-128 in the Clarks Fork Basin, Wyoming: left dentary with P_4-M_1 in occlusal (A), lateral (B), and medial views (C).

This gives the talonid notch a distinctly U-shaped outline in lingual view. None of the currently available specimens of *Viverravus rosei* have an M_2 with a visible crown.

The length of P^3 is considerably shorter than that of P^4. It has a tall main cusp and small anterior and posterior accessory cusps on the parastyle and metastyle respectively. There is no protocone. P^4 is triangular in outline with a shorter metastyle blade than in other species of the genus. The paracone is tall and the protocone is not visible in any known specimen. There is a labial cingulum running from the cusp on the parastyle to the posterior end of the metastyle and a deep metastylar notch. UM 92284 is the only specimen containing upper molars—only the labial portion of M^1 is visible. The stylar shelf is narrow, and there is a large parastylar hook, similar to that found in other species of the genus. There is no metastylar blade, and the metacone, which is considerably smaller than the paracone, is positioned close to the posterolabial corner of the tooth. Neither the protocone nor the conules are visible.

UM 92284 contains most of the skull region directly dorsal to the posterior premolars and the molars, but it is quite crushed. Broken remnants of the anterior portion of the zygomatic arch are also present in this specimen, but they have been displaced from their life position. Only extensive micropreparation and reconstruction of this specimen will allow more to be said about it.

TABLE 4—Summary of measurements of the upper and lower cheek teeth of *Viverravus rosei* from the Bighorn and Clarks Fork Basins, Wyoming. Specimens included here are from the late Clarkforkian (Cf-3) through middle Wasatchian (Wa-4). A decrease in the size of the species through this time (see text) contributes to its overall variability (see Figure 7). For this reason, measurements have been tabulated by faunal zone. All measurements in millimeters.

Tooth position	N	Observed range	Mean	Standard deviation	Coefficient of variation
			Cf-3		
Upper dentition					
P^4 L	1	2.11	—	—	—
P^4 W	—	—	—	—	—
M^1 L	1	1.47	—	—	—
M^1 W	—	—	—	—	—
Lower dentition					
P_4 L	1	2.01	—	—	—
P_4 W	1	0.40	—	—	—
M_1 L	1	2.04	—	—	—
M_1 W	—	—	—	—	—
M_2 L	1	1.00	—	—	—
M_2 W	—	—	—	—	—
			Wa-2		
Lower dentition					
P_4 L	2	2.80 - 3.12	—	—	—
P_4 W	2	1.08 - 1.09	—	—	—
M_1 L	1	3.33	—	—	—
M_1 W	1	1.84	—	—	—
			Wa-3		
Lower dentition					
P_4 L	1	2.65	—	—	—
P_4 W	1	0.97	—	—	—
M_1 L	2	2.92 - 2.96	—	—	—
M_1 W	2	1.70 - 1.79	—	—	—
M_2 L	1	1.79	—	—	—
M_2 W	1	1.09	—	—	—
			Wa-4		
Lower dentition					
P_4 L	2	2.07 - 2.96	—	—	—
P_4 W	2	0.99 - 1.14	—	—	—
M_1 L	1	3.04	—	—	—
M_1 W	1	1.65	—	—	—
			All faunal zones		
Upper dentition					
P^4 L	1	2.11	—	—	—
P^4 W	—	—	—	—	—
M^1 L	1	1.47	—	—	—
M^1 W	—	—	—	—	—
Lower dentition					
P_4 L	6	2.01 - 3.12	2.60	0.4629	17.79
P_4 W	6	0.40 - 1.14	0.95	0.2746	29.06
M_1 L	5	2.04 - 3.33	2.86	0.4846	16.96
M_1 W	4	1.65 - 1.84	1.75	0.0858	4.92
M_2 L	2	1.00 - 1.79	—	—	—
M_2 W	1	1.09	—	—	—

Parts of the post-cranial skeleton are also preserved in UM 92284, but these are partially embedded in a nodule. Furthermore, they are mixed with remains of other species, including frogs. This makes the association of elements that have been completely removed from the nodule somewhat suspect. The bulk of the postcrania preserved in this nodule, however, do seem to belong to the same individual as the skull. Most of this material consists of five articulated lumbar vertebrae, with a variety of other bones accreted onto them. A distal humeral fragment also seems to belong to *Viverravus rosei*. Its width, from entepicondyle to ectepicondyle, is 2.95 mm. The entepicondyle projects medially well away from the trochlea and there is an entepicondylar foramen present. The supinator crest is large and creates a graceful arc curving proximally from the ectepicondyle. The capitulum is rounded and projects anteriorly from the main body of the distal humerus. The trochlea has a distinct ridge along its medial border. The coronoid fossa is deeper than the olecranon fossa and there is no open supratrochlear foramen, although the bone in the fossa is quite thin.

Measurements of the posterior cheek teeth of *Viverravus rosei* are presented in Table 4.

Viverravus politus Matthew and Granger, 1915

Figs. 11, 12

Viverravus politus Matthew and Granger, 1915, p. 28, fig. 23. Bown, 1979, p. 95. Rose, 1981, p. 101. Gingerich, 1989, p. 39.

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

Protictis schaffi Gingerich and Winkler, 1985, p. 110, figs. 10-11.

Holotype.—AMNH 16113, mandible fragment with right M_{1-2}, left P_4-M_2.

Type locality.—Sandcoulee beds north of Ralston in the Clarks Fork Basin, Wyoming. According to Gingerich (1989) this locality is probably younger than Wa-0 (early Sandcouleean).

Age and distribution.—Late Tiffanian (late Paleocene) through early Wasatchian land-mammal ages (early Eocene) of western North America.

Definition.—An evolutionary species consisting of the series of ancestor-descendant populations occurring between speciation (cladogenic) events that contains the holotype of *V. politus* (AMNH 16113).

Diagnosis.—A large species of *Viverravus* which differs from all others in having a small, single-rooted P_1, in having a relatively small P_3 with only a single posterior accessory cusp, in having an M_1 on which the metaconid is positioned far posteriorly giving the trigonid a very open appearance in lingual view, and in having a proportionally long P^4 with a small, anteriorly placed protocone.

Referred specimens.—**Early Clarkforkian** [Cf-1]: **SC- 257**: UM 73360. **Middle Clarkforkian** [Cf-2]: **SC-52**: UM 71580. **SC-115**: UM 83209. **SC-195**: UM 69336 and 102460. **SC-201**: UM 69270. **SC-202**: UM 83760. **SC-214**: UM 69884. **Late Clarkforkian** [Cf-3]: **SC-23**: UM 65118 and 65125. **SC-24**: UM 65088. **SC-57**: UM 65653. **SC-70**: UM 66853. **SC-107**: UM 66618. **SC-230**: UM 71424. **SC-233**: UM 71477. **Early Sandcouleean** [Wa-0]: **SC-067**: UM 87857. **Middle Sandcouleean** [Wa-1]: **SC-4**: UM 64636, 67364, and 72889. **SC-15**: UM 81942. **SC-26**: UM 65329. **SC-40**: UM 80384. **SC-125**: UM 66871. **SC-182**: UM 68770. **Late Sandcouleean** [Wa-2]: **SC-2**: UM 101743. **SC-46**: UM 86365. **SC-88**: UM 76540. **Early Graybullian** [Wa-3]: **MP-138**: UM 93255. **SC-192**: UM 73881. **Middle Graybullian** [Wa-4]: **SC-111**: UM 66683. **SC-255**: UM 74526.

Description.—There are more than 30 specimens of *Viverravus politus* in the University of Michigan collections from the Bighorn and Clarks Fork basins, adding significantly to our knowledge of this species. The new material consists primarily of dentary fragments containing posterior cheek teeth, but also three fragmentary maxillae containing the posterior cheek teeth. None of these specimens contain incisors nor their alveoli, but indicate that the dental formula of the cheek teeth was $C^1_1\ P^4_4\ M^2_2$. P_1 was single-rooted, but the other lower premolars were

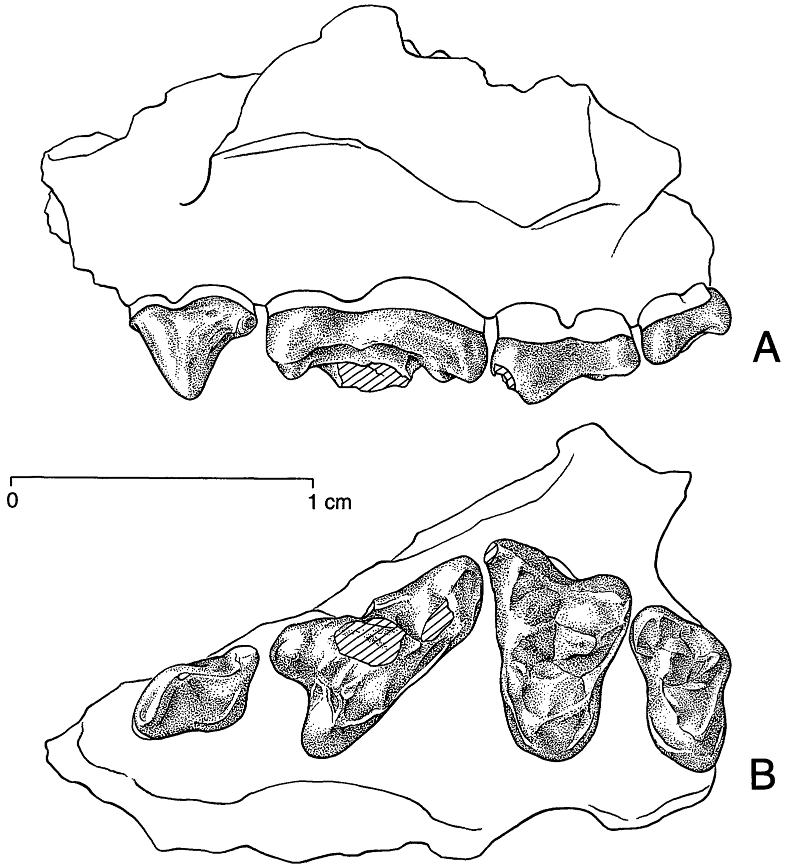


FIG. 11—Upper dentition of *Viverravus politus* from the Clarks Fork Basin, Wyoming: left upper dentition (UM 81942, SC-15) with P^3-M^2 in lateral (A) and occlusal (B) views.

double-rooted. Only P^{3-4} are preserved in the Michigan specimens, but the Princeton cranium (PU 16495) described by Gingerich and Winkler (1985) under the name *Protictis schaffi* indicates that P^{1-3} were double-rooted, while P^4 was three-rooted. The mandible was relatively deep beneath the molars, more so in specimens from younger than from older horizons.

The crown of P^3 is small relative to that of P^4. (The ratio of the length of P^3 to the length of P^4 is about 0.63. In *Viverravus acutus* this same ratio is about 0.86.) The relatively small size of the P^3 is more pronounced in specimens from later horizons than from earlier ones. The central cusp of the tooth is high and somewhat laterally compressed. There are tiny anterior and posterior accessory cusps, but no basal cingula. The lingual base of the tooth is slightly swollen just posterior to the base of the central cusp. P^4 is triangular in outline and relatively long anteroposteriorly, both in comparison to P^3 and to the molars. The metastyle blade is long with a pronounced notch. The protocone is small and positioned such that its cusp is anterior to the paracone cusp. The parastyle cusp is also small and positioned either directly anterior to the paracone or slightly lingual to it. An indistinct cingulum, which is only variably present, runs along the labial base of the tooth connecting the parastyle with the posterior point of the metastyle blade. A lingual cingulum connects the protocone with the metastyle blade. A third cingulum runs from the protocone to the parastyle, but it is indistinct

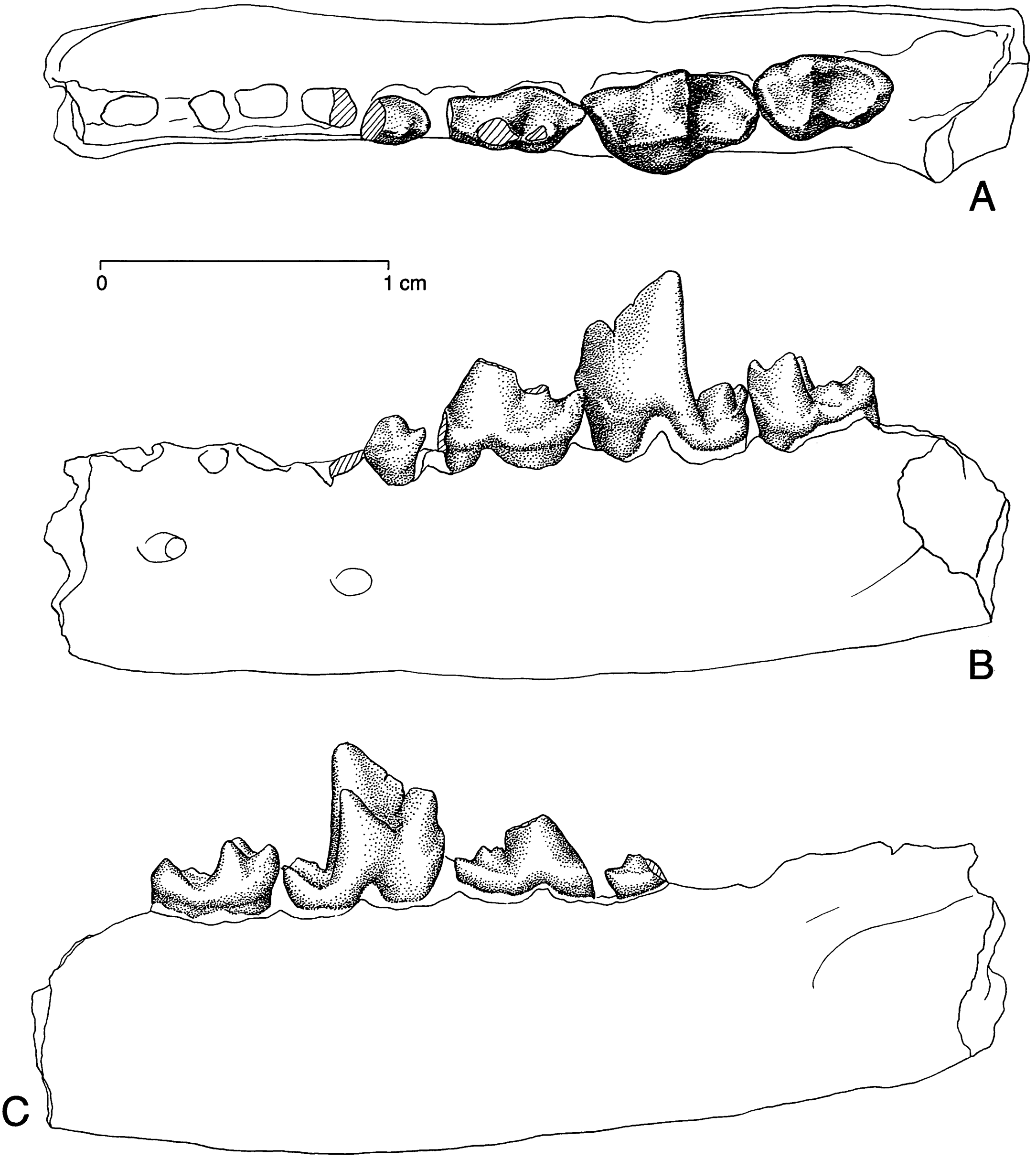


FIG. 12—Lower dentition of *Viverravus politus* from the Clarks Fork Basin, Wyoming: left lower dentition (UM 65118, SC-23) with a fragment of P_3 and P_4-M_2 in occlusal (A), lateral (B), and medial views (C).

and has a deep flexus bending it posteriorly to the anterior base of the paracone. All of these cingula extend to the apices of the various cusps and are not continuous around their bases.

The M^1 of *Viverravus politus* is triangular in occlusal outline. The parastyle is large and hooked, while the metastyle is much smaller. There is a shallow ectoflexus between the two and a stylar shelf of medium width. The paracone is somewhat larger than the metacone, the former positioned slightly lingual to the latter. There is a large, distinct paraconule, but no

TABLE 5—Summary of measurements of the upper and lower posterior cheek teeth of *Viverravus politus* from the Bighorn and Clarks Fork Basins, Wyoming. Specimens included here are from the middle Clarkforkian (Cf-2) through middle Wasatchian (Wa-4). An increase in the size of the species through this time contributes to its high level of variability (see Figure 7). For this reason, measurements are also listed by faunal zone. All measurements in millimeters.

Tooth position	N	Observed range	Mean	Standard deviation	Coefficient of variation
			Cf-2		
Upper dentition					
M^1 L	2	4.27 - 4.88	—	—	—
W	2	6.64 - 6.78	—	—	—
Lower dentition					
P_4 L	3	4.84 - 5.42	5.05	—	—
W	3	2.00 - 2.41	2.17	—	—
M_1 L	4	5.42 - 6.01	5.72	0.2685	4.69
W	4	3.27 - 3.67	3.42	0.1780	5.20
M_2 L	5	3.88 - 4.52	4.36	0.2704	6.20
W	5	2.49 - 2.84	2.69	0.1335	4.97
			Cf-3		
Lower dentition					
P_4 L	4	4.28 - 4.46	4.38	0.0800	1.74
W	4	1.60 - 1.99	1.77	0.1700	9.59
M_1 L	2	4.46 - 4.62	4.54	—	—
W	2	2.67 - 2.82	2.75	—	—
M_2 L	2	3.17 - 3.30	3.24	—	—
W	2	1.89 - 2.08	1.99	—	—
			Wa-0		
Lower dentition					
M_1 L	1	4.58	—	—	—
W	1	5.70	—	—	—
			Wa-1		
Upper dentition					
P^4 L	2	7.05 - 7.08	—	—	—
W	2	5.97 - 6.92	—	—	—
M^1 L	3	4.55 - 4.82	4.69	—	—
W	3	7.35 - 7.91	7.70	—	—
M^2 L	3	3.07 - 3.63	3.33	—	—
W	3	5.31 - 5.98	5.75	—	—
Lower dentition					
P_4 L	2	5.22 - 5.82	—	—	—
W	2	2.33 - 2.72	—	—	—
M_1 L	3	6.16 - 7.29	6.65	—	—
W	3	3.94 - 4.20	4.09	—	—
M_2 L	4	5.20 - 5.41	5.29	0.1034	1.96
W	4	3.06 - 3.26	3.18	0.0968	3.05
			Wa-2		
Lower dentition					
P_4 L	1	5.44	—	—	—
W	1	2.65	—	—	—
M_1 L	1	8.15	—	—	—
W	1	4.72	—	—	—
M_2 L	1	3.34	—	—	—
W	1	1.80	—	—	—

			Wa-3			
Upper dentition						
M^1	L	1	4.47	—	—	—
	W	1	6.11	—	—	—
Lower dentition						
P_4	L	1	5.46	—	—	—
	W	1	2.72	—	—	—
M_1	L	1	8.53	—	—	—
	W	1	4.98	—	—	—
M_2	L	1	4.35	—	—	—
	W	1	2.45	—	—	—
			Wa-4			
Upper dentition						
P^4	L	2	6.42 - 6.93	—	—	—
	W	2	6.20 - 6.47	—	—	—
M^1	L	2	4.09 - 4.24	—	—	—
	W	2	6.38 - 7.03	—	—	—
			All faunal zones			
Upper dentition						
P^4	L	4	6.42 - 7.08	6.87	0.3069	4.47
	W	4	5.97 - 6.92	6.39	0.4082	6.39
M^1	L	9	4.09 - 4.88	4.51	0.2694	5.97
	W	9	5.70 - 7.91	6.86	0.7505	10.94
M^2	L	3	3.07 - 3.63	3.33	0.2829	8.50
	W	3	5.31 - 5.98	5.75	0.3812	6.63
Lower dentition						
P_4	L	11	4.28 - 5.82	4.96	0.5368	10.81
	W	11	1.60 - 2.72	2.18	0.4103	18.80
M_1	L	11	4.46 - 8.35	6.22	1.2792	20.57
	W	11	2.67 - 4.98	3.74	0.7348	19.64
M_2	L	13	3.17 - 5.41	4.39	0.7807	17.77
	W	13	1.80 - 3.26	2.64	0.4893	18.52

metaconule. Both pre- and postcingula are present. The postcingulum is located closer to the base of the crown than the precingulum, and the former is labially continuous (or almost continuous in early specimens) with the postprotocrista at the posterior edge of the talon basin. The labial end of the precingulum, however, is dorsal to the preparaconule crista and does not approach the rim of the talon basin. In most specimens, the pre- and postcingula are not continuous around the base of the protocone. The preparaconule crista extends labially onto the base of the parastyle blade. The protocone is somewhat asymmetrical anteroposteriorly such that it appears to be leaning anteriorly in labial view. In early specimens the protocone is broader than in later ones. The M^2 is considerably smaller than the M^1, a trend that becomes more pronounced in younger specimens. Many of the features of the M^2 are similar to those of the M^1: the paracone is larger than the metacone, there is no metaconule, and the postcingulum intersects the posterior border of the talon basin. The parastyle is shorter on the M^2, however, and the stylar shelf is narrower.

P_1 is small and single-rooted with a single, conical cusp making up its crown. P_2 is two-rooted with one large cusp making up the crown and a small cusp at its posterior margin. P_3 is similar in morphology to P_2 except that it has both first and second posterior accessory cusps in addition to the main cusp. P_3 is short compared to P_4. The latter is large and two-rooted with a large main cusp as well as an anterior accessory cusp and first and second posterior accessory cusps. There are notches on the labial side of the tooth between the main and the first posterior accessory cusps and between the first and second posterior accessory cusps. A posterior cingulid runs anterolingually from the second posterior accessory cusp, rimming a small basin located posterior to the main cusp and lingual to the first posterior accessory cusp. This cingulid ends at the posterior margin of the main cusp. There are two faint cingulids along the labial base of the tooth just above each root.

M_1 is the largest of the lower cheek teeth. The trigonid is high and open. The protoconid is the highest of the talonid cusps and the paraconid and metaconid are roughly equal in height. The metaconid curves posteriorly and the paraconid is inclined anteriorly. These combine to give the trigonid an open morphology in lingual view. The carnassial notch of the paracristid is positioned closer to the paraconid than to the protoconid. This gives the posterior portion of the cristid a gentle slope, which gives the protoconid the appearance of pointing posteriorly. There is a small precingulid on the anterolabial base of the tooth. The talonid basin is narrow and has two main cusps, the hypoconid and hypoconulid, with a small notch between them. The lack of an entoconid gives the talonid basin a posterolabially angled orientation. The entocristid is continuous across the lingual side of the basin and connects along the back of the trigonid with the metaconid. The cristid obliqua ends against the back of the trigonid at the base of the protoconid. A small cingulid runs anteriorly from the hypoconulid along the labial base of the talonid to the hypoflexid.

M_2 is smaller than M_1 and its trigonid is much lower. The protoconid is slightly taller than the metaconid and paraconid, but the three are almost equal in height. The talonid is relatively long and the hypoconulid is its tallest cusp. There is no entoconid nor is there a cingulid running on the labial surface of the tooth.

Measurements of the cheek teeth of Clarkforkian and Wasatchian *Viverravus politus* are presented in Table 5.

Didymictis Cope, 1875

Didymictis Cope, 1875, p. 5.
Protictis (in part), Gingerich and Winkler, 1985, p. 103.

Type species.—Didymictis protenus (Cope, 1874).

Included species.—Didymictis altidens, Cope 1880; *D. proteus*, Simpson, 1937; *D. leptomylus*, Cope, 1880; *D. protenus*, (Cope, 1874); and *D. vancleveae*, Robinson, 1966.

Age and distribution.—Tiffanian (late Paleocene) through Gardnerbuttean (earliest Eocene) of North America.

Didymictis proteus Simpson, 1937

Fig. 13

Didymictis protenus proteus Simpson, 1937, p. 13, fig. 6. Rose, 1981, p. 98.
Didymictis dellensis Dorr, 1952, p. 85.
Didymictis ?undescribed species, Rose, 1981, p. 99, fig. 47.
Didymictis ?sp. nov., Rose, 1981, p. 156.
Protictis dellensis, Gingerich and Winkler, 1985, p. 117.
Didymictis leptomylus, Gingerich, 1989, p. 39.

Holotype.—AMNH 16071, fragments of the right and left jaws containing right P_4 and M_2 and a fragment of the left M_1.

Type locality.—Head of Big Sand Coulee.

Age and Distribution.—Late Tiffanian (late Paleocene) through earliest Wasatchian (earliest Eocene) of Wyoming.

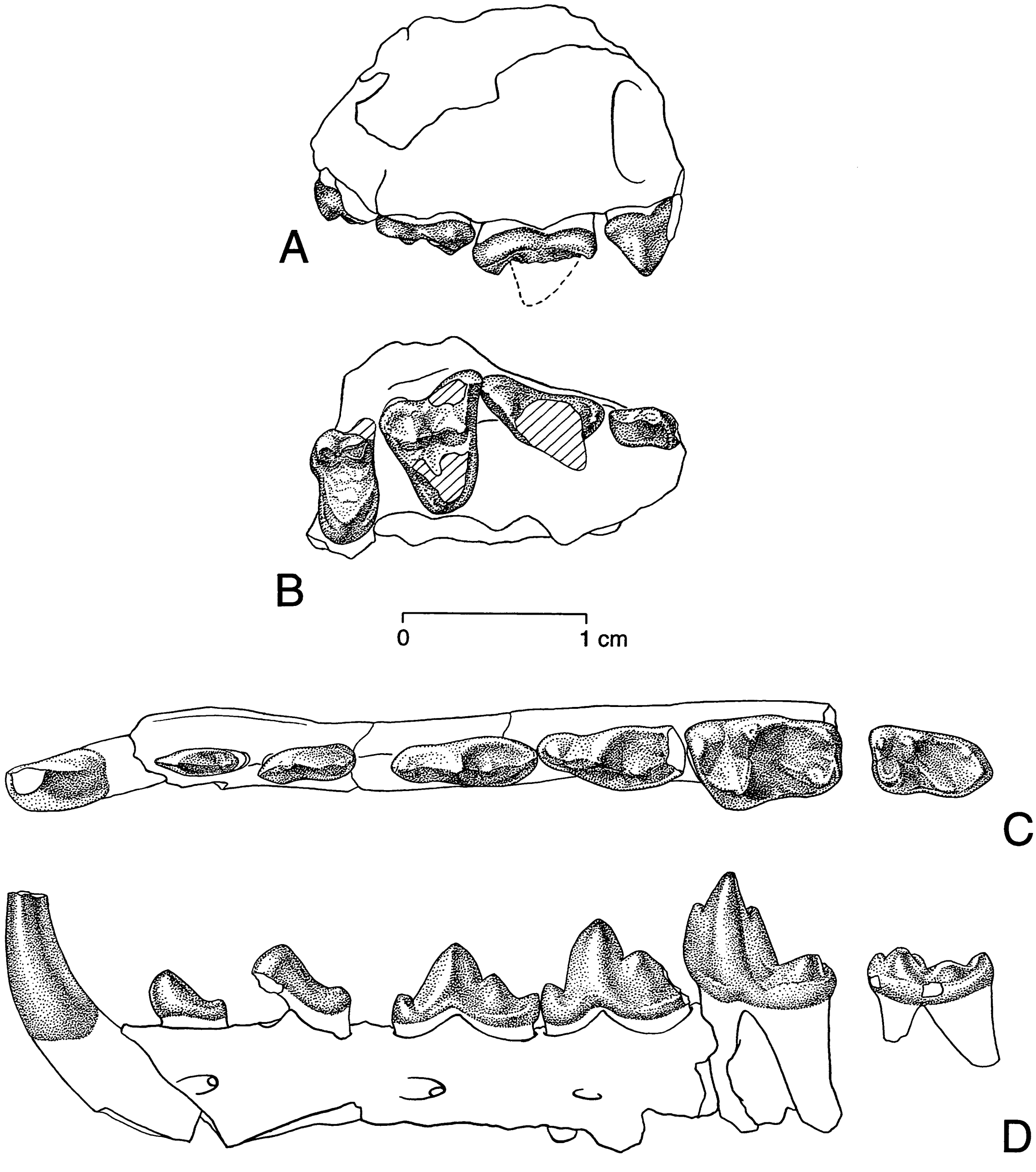


FIG. 13—Upper and lower dentitions of *Didymictis proteus* from the Clarkforkian of the Clarks Fork Basin, Wyoming: right maxilla fragment (UM 73714, SC-260) with P^3-M^2 in lateral (A) and occlusal views (B), and left dentary (UM 68432, SC-173) with C_1-M_2 in occlusal (C) and lateral views (D).

Definition.—An evolutionary species consisting of the series of ancestor-descendant populations between speciation (cladogenic) events that contains the holotype (AMNH 16071).

Diagnosis.—Differs from *Didymictis leptomylus* in being slightly larger (except in Wa-0) and differs from *D. protenus* in being slightly smaller. It is the only species of *Didymictis* in the Tiffanian and Clarkforkian.

TABLE 6—Summary of measurements of the upper and lower cheek teeth of *Didymictis proteus* from the Bighorn and Clarks Fork Basins, Wyoming. Specimens included here are from the early Clarkforkian (Cf-1) through earliest Wasatchian (Wa-0). Change in the size of the species through this time contributes to its variability (see Figure 8). Because of this, measurements are also tabulated by faunal zone. All measurements in millimeters.

Tooth position	N	Observed range	Mean	Standard deviation	Coefficient of variation
			Cf-1		
Upper dentition					
P^4 L	1	7.51	—	—	—
W	1	8.86	—	—	—
M^1 L	2	5.33 - 6.39	—	—	—
W	2	8.00 - 8.56	—	—	—
M^2 L	2	3.80 - 4.13	—	—	—
W	2	6.32 - 7.07	—	—	—
Lower dentition					
P_4 L	2	8.19 - 8.60	8.40	—	—
W	2	3.33 - 3.43	3.38	—	—
M_1 L	3	7.97 - 8.37	8.13	—	—
W	3	4.74 - 5.05	4.94	—	—
M_2 L	1	6.79	—	—	—
W	1	3.45	—	—	—
			Cf-2		
Upper dentition					
P^4 L	4	7.50 - 8.41	8.12	0.4258	5.25
W	4	8.73 - 9.54	9.05	0.3450	3.81
M^1 L	9	6.17 - 7.15	6.79	0.3423	5.04
W	9	8.77 -10.47	9.58	0.5897	6.16
M^2 L	5	4.16 - 4.77	4.40	0.2726	6.20
W	5	6.80 - 7.35	7.15	0.2259	3.16
Lower dentition					
P_4 L	9	8.11 - 9.54	8.99	0.4666	5.19
W	9	3.33 - 4.10	3.75	0.2934	7.82
M_1 L	20	8.09 -10.11	9.17	0.4691	5.12
W	20	5.06 - 6.16	5.66	0.3087	5.45
M_2 L	24	6.18 - 8.76	7.84	0.6005	7.66
W	24	3.70 - 5.12	4.47	0.2922	6.54
			Cf-3		
Upper dentition					
P^4 L	1	7.72	—	—	—
W	1	8.07	—	—	—
M^1 L	6	7.02 - 7.86	7.50	0.3003	4.00
W	6	9.30 -10.34	9.88	0.3339	3.38
M^2 L	2	4.47 - 4.96	—	—	—
W	2	7.49 - 7.62	—	—	—
Lower dentition					
P_4 L	5	6.99 - 9.31	8.09	0.9593	11.86
W	5	2.52 - 3.55	3.17	0.4823	15.22
M_1 L	9	9.10 - 9.97	9.51	0.3492	3.67
W	9	5.25 - 5.90	5.60	0.2181	3.89
M_2 L	8	7.51 - 8.51	7.93	0.4451	5.61
W	8	3.92 - 4.69	4.36	0.2577	5.91

				Wa-0		
Lower dentition						
P_4	L	2	8.00 - 8.56	—	—	—
	W	2	3.88 - 3.93	—	—	—
M_1	L	3	7.32 - 8.34	7.77	—	—
	W	3	4.53 - 4.90	4.77	—	—
M_2	L	4	5.98 - 6.93	6.58	0.4410	6.70
	W	4	3.31 - 4.12	3.76	0.3354	8.92
				All faunal zones		
Upper dentition						
P^4	L	6	7.54 - 8.41	7.95	0.4249	5.34
	W	6	8.07 - 9.54	8.86	0.4753	5.37
M^1	L	17	5.33 - 7.86	6.93	0.6308	9.10
	W	17	8.00 -10.47	9.53	0.6787	7.12
M^2	L	9	3.80 - 4.69	4.37	0.3609	8.25
	W	9	6.32 - 7.62	7.14	0.3929	5.50
Lower dentition						
P_4	L	18	6.99 - 9.54	8.60	0.7132	8.30
	W	18	2.52 - 4.10	3.57	0.4223	11.84
M_1	L	35	7.32 -10.11	9.05	0.6739	7.45
	W	35	4.53 - 6.16	5.51	0.4017	7.29
M_2	L	37	5.98 - 8.76	7.70	0.6881	8.94
	W	37	3.31 - 5.12	4.34	0.3833	8.83

Referred specimens.—**Late Tiffanian** [Ti-5]: **Dell Creek Quarry:**: UM 27232. **Early Clarkforkian** [Cf-1]: **SC-173**: UM 68432. **SC-198**: UM 69241. **SC-248**: UM 71792. **SC-259**: UM 73370. **SC-260**: UM 73381 and 73714. **Middle Clarkforkian** [Cf-2]: **SC-19**: UM 65013 and 80271. **SC-21**: UM 65057. **SC-29**: UM 65241 and 86259. **SC-52**: UM 71586. **SC-58**: UM 65658, 65665, and 65667. **SC-62**: UM 65777 and 83207. **SC-74**: UM 71181. **SC-84**: UM 66209. **SC-100**: UM 66543. **SC-116**: UM 66712 and 66715. **SC-117**: UM 87800. **SC-120**: UM 66764 and 67017. **SC-127**: UM 66915 and 71585. **SC-136**: UM 69907. **SC-143**: UM 80559, 83013, 86547, and 87825. **SC-163**: UM 68227. **SC-164**: UM 68248 and 68249. **SC-188**: UM 71606 and 68865. **SC-195**: UM 69177, 69869, 102457, 102458, and 102459. **SC-197**: UM 69225. **SC-201**: UM 69316 and 69317. **SC-205**: UM 69325. **SC-234**: UM 71438, 71453, 71458, and 71460. **SC-238**: UM 71636 and 71637. **Late Clarkforkian** [Cf-3]: **SC-57**: UM 65656. **SC-153**: UM 67452. **Early Sandcouleean** [Wa-0]: **SC-67**: UM 71765, 71766, 83623, 83630, 83635, 83636, 83661, 83664, 85590, 86003, 87859, and 92356.

Description.—Material referred here to the species *Didymictis proteus* was described by Gingerich and Winkler (1985) from the Tiffanian, by Bown (1979) and Rose (1981) from the Clarkforkian, and by Gingerich (1989) from the earliest Wasatchian. The dental formula of *Didymictis proteus* is $I^?_?$ C^1_1 P^4_4 M^2_2. The premolars are not tightly spaced in adults. P_1 is robust with two roots. The single cusp of its crown is positioned above the anterior root. P_2 is larger than P_1, but also single-cusped. In some specimens a tiny posterior accessory cusp is present. P_3 is larger than both P_1 and P_2 and has a somewhat more complex morphology. Its crown consists of a large, centrally located main cusp as well a small anterior accessory cusp and both first and second posterior accessory cusps. There is a small notch between the main cusp and the first posterior accessory cusp. The second posterior accessory cusp is winged by cingulids that extend anteriorly to the lateral and medial sides of the base of the main cusp. P_4 is the largest of the lower premolars and has the same number of cusps as does P_3. The main cusp, however, is proportionally taller and more massive, as are the accessory cusps. A cingulid runs the anteroposterior length of the tooth beginning at the apex of the anterior accessory cusp. This cingulid runs down the posterior surface of this cusp, up the anterior surface of the main cusp, down its posterior face, up and down the anterior and posterior surfaces of the first posterior accessory cusp, and up the anterior surface of the second posterior accessory cusp.

The cingulid is interrupted between the anterior accessory cusp and the main cusp, between the main cusp and the first posterior accessory cusp, and between the first and second posterior accessory cusps by notches. Cingulids run anteriorly from the second posterior accessory cusp on both the labial and lingual sides of the tooth to the base of the main cusp. On the lingual side, the cingulid forms a small basin that is bounded on its labial side by the first posterior accessory cusp.

M_1 of *Didymictis proteus* is large with a high trigonid and well developed talonid. The protoconid is the tallest cusp and the paraconid and metaconid are subequal in height. The latter cusps are close together, giving the trigonid a closed appearance when viewed from the labial side. The talonid cusps consist of an entoconid, hypoconulid, and hypoconid. The hypoconid is the largest of these and the hypoconulid the smallest. The entoconid and hypoconulid are positioned closely together at the posterolabial margin of the talonid basin. A cingulid runs around the labial margin of the talonid basin from the apex of the hypoconulid, around the base of the hypoconid, anteriorly across the base of the hypoflexid, to the posterolabial margin of the protoconid. In some specimens, it is continuous anteriorly with the precingulid, which rises along the anterior margin of the protoconid. The entocristid is continuous from the entoconid to the apex of the metaconid. M_2 is much smaller than M_1. The trigonid cusps of the former are much lower than in the latter and the talonid is much longer. The protoconid, paraconid, and metaconid are all subequal in height, and the latter two are, like those of M_1, positioned closely together. There is a strong cingulid around the labial base of the crown beginning anteriorly at the precingulid and continuing posteriorly ending at the apex of the hypoconulid. The hypoconulid itself is much larger than that of M_1 and it is positioned far posteriorly on the talonid.

The upper premolars, like the lowers, are not tightly appressed in adults. P^1 is small, two-rooted, and single-cusped. P^2 is somewhat larger, but also with two roots. In some specimens there is an indistinct cingulum along the lingual base of the crown. P^3, also two-rooted, is a larger tooth with a large main cusp, a smaller posterior accessory cusp, and a tiny anterior accessory cusp. There is a slight lingual swelling at the base of the crown just posterior to the base of the main cusp. The entire base of the tooth crown is rimmed by a cingulum. A notch is present between the main cusp and the posterior accessory cusp. P^4, like those of most carnivorans, is semi-molariform and forms the upper half of the carnassial set of teeth. It is three-rooted with a large protocone, along with an anterior parastyle cusp, a paracone, and a metastyle cusp. The metastyle blade is long with a deep notch. The parastyle is relatively shorter, but also has a notch between its cusp and the paracone. Almost the entire base of the tooth is rimmed by a cingulum, although it is not present between the lingual-most point of the protocone and the parastyle.

M^1 is sub-triangular in shape with a protocone, metacone, paracone, parastyle, and metastyle. The metastyle is small, but the parastyle forms a large lingual wing. There are heavy pre- and postprotocingula as well as a heavy cingulum along the margin of the stylar shelf that is continuous with the postmetaconule crista. The pre- and postprotocingula are not generally continuous around the base of the protocone. There is no metastyle cusp, but there is a large parastyle cusp. The paracone and metacone are subequal in height, but the metacone is considerably shorter and smaller than the paracone. The preparacrista contains a notch between the parastyle cusp and the paracone. The paraconule and metaconule are about the same size and both well developed with both pre- and post-cristae. M^2 is significantly smaller than M^1. It is also triangular in outline, but the parastyle is much shorter than that of M^1. The protocone is the largest cusp and the metacone is significantly smaller than the paracone. There is a very small, conical parastyle cusp anterolabial to the metacone. Both the metaconule and paraconule are well developed and winged. The preparconule crista extends labially, connecting at the parastyle with a cingulum running the length of the stylar shelf, which in turn connects with the postmetaconule crista at the metastyle. Both the pre- and postprotocristae are large, but they do not connect at the base of the protocone.

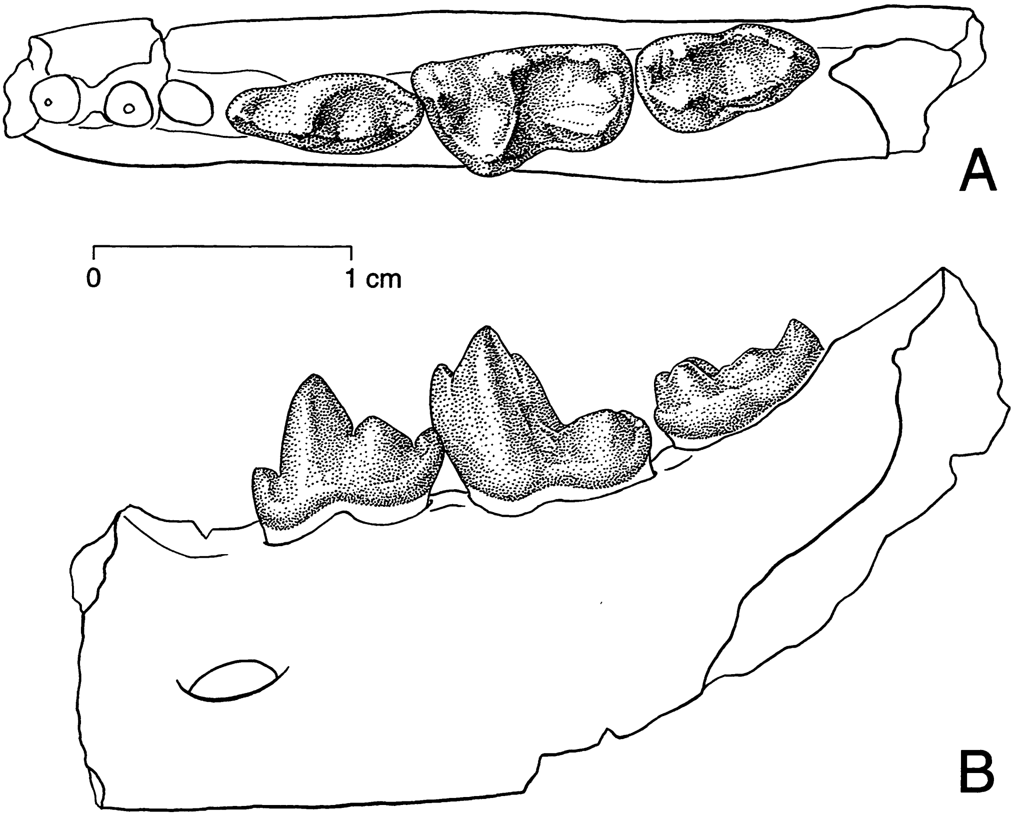


FIG. 14—Lower dentition of *Didymictis leptomylus* from the Wasatchian of the Clarks Fork Basin, Wyoming: left dentary with P_4-M_2 (UM 76527, SC-87) in occlusal (A) and lateral views (B).

Measurements of the posterior cheek teeth of *Didymictis proteus* from the Clarkforkian and earliest Wasatchian are presented in Table 6.

Didymictis leptomylus Cope, 1880

Fig. 14

Didymictis leptomylus Cope, 1880, p. 908; 1883, p. 309, plate 25a, fig. 12.
Didymictis protenus, McKenna, 1960, p. 95.
Didymictis protenus (in part), Bown, 1979, p. 93 (small variety). Davidson, 1987, p. 119.

Holotype.—AMNH 4238.

Type locality.—The type of *Didymictis leptomylus* was collected somewhere in the Bighorn Basin according to Cope (1883), although he originally reported as coming from the Wind River Basin (Cope, 1880). Field work by parties from the University of Michigan indicate that the specimen probably came from horizons assigned to an early Wasatchian age (Wa-1 or Wa-2) (Gingerich, personal communication).

Age and distribution.—Early Wasatchian (Wa-1-Wa-3) of western North America.

TABLE 7—Summary of measurements of the upper and lower cheek teeth of Didymictis leptomylus from the Bighorn and Clarks Fork Basins, Wyoming. Specimens included here are from the early (Wa-1) through middle Wasatchian (Wa-3). Change in the size of the species through this time contributes to its variability (see Figure 8). Because of this, measurements are also tabulated by faunal zone. All measurements in millimeters.

Tooth position	N	Observed range	Mean	Standard deviation	Coefficient of variation
		Wa-1			
Upper dentition					
M^1 L	3	6.35 - 7.24	6.70	—	—
W	3	9.37 - 9.64	9.50	—	—
M^2 L	1	4.54	—	—	—
W	1	6.39	—	—	—
Lower dentition					
P_4 L	4	7.71 - 9.42	8.37	0.7829	9.35
W	4	2.85 - 3.54	3.32	0.3179	9.57
M_1 L	7	7.96 -10.14	9.27	0.7643	8.24
W	7	4.82 - 5.62	5.31	0.2762	5.20
M_2 L	6	6.97 - 7.77	7.41	0.3030	4.09
W	6	3.96 - 4.15	4.07	0.0857	2.11
		Wa-2			
Lower dentition					
P_4 L	1	6.98	—	—	—
W	1	3.17	—	—	—
M_1 L	5	7.23 - 8.92	8.20	0.6886	8.40
W	5	4.24 - 5.04	4.75	0.3487	7.34
M_2 L	3	6.40 - 7.88	7.05	—	—
W	3	3.70 - 4.18	3.87	—	—
		Wa-3			
Lower dentition					
P_4 L	1	6.82	—	—	—
W	1	2.87	—	—	—
M_1 L	1	6.60	—	—	—
W	1	4.45	—	—	—
M_2 L	1	6.04	—	—	—
W	1	3.45	—	—	—
		All faunal zones			
Upper dentition					
M^1 L	3	6.35 - 7.24	6.70	0.4725	7.05
W	3	9.37 - 9.64	9.50	0.1353	1.42
M^2 L	1	4.54	—	—	—
W	1	6.39	—	—	—
Lower dentition					
P_4 L	6	6.82 - 9.42	7.88	0.9729	12.35
W	6	2.85 - 3.54	3.22	0.3067	9.52
M_1 L	13	6.60 -10.14	8.65	1.0544	12.18
W	13	4.24 - 5.62	5.03	0.4324	8.60
M_2 L	10	6.04 - 7.88	7.16	0.6018	8.40
W	10	3.45 - 4.18	3.94	0.2436	6.18

Definition.—An evolutionary species consisting of the series of ancestor-descendant populations between speciation (cladogenic) events that contains the holotype of *Didymictis leptomylus* (AMNH 4238).

Diagnosis.—Differs from *Didymictis protenus* in being smaller in all linear measurements and differs from earliest Wasatchian *D. proteus* in being slightly larger.

Referred specimens.—**Middle Sandcouleean** [Wa-1]: **SC-4**: UM 67374, 72881, and 72882. **SC-7**: UM 65162. **SC-17**: UM 64958. **SC-26**: UM 80771 and 80775. **SC-39**: UM 76827. **SC-40**: UM 87550. **SC-161**: UM 77459 and 77486. **SC-182**: UM 68760 and 68764. **SC-206**: UM 69417. **SC-316**: UM 80193 and 101802. **Late Sandcouleean**[Wa-2]: **SC-46**: UM 86430. **SC-54**: UM 80092. **SC-87**: UM 76527. **SC-133**: UM 68481 and 68472. **SC-311**: UM 76631. **Early Graybullian** [Wa-3]: **MP-149**: UM 93654.

Description.—This species is known from far fewer specimens than the earlier *Didymictis proteus*, but is similar in most aspects of its morphology. There are no incisors or anterior premolars preserved in any of the UM specimens. P_4 is a large tooth subequal in length to M_1. It has four cusps: an anterior accessory cusp, a main cusp, and first and second posterior accessory cusps. There is a cristid running the length of the tooth which connects the apices of all four cusps. A labial cingulid runs along the base of the tooth from the second posterior accessory cusp to the anterior accessory cusp. It is heavier at its posterior end and, in some specimens, indistinct at its anterior end. M_1 has a high trigonid. The protoconid is the tallest cusp and the paraconid and metaconid are subequal in height. There is no hypoconulid. A cingulid runs from the entoconid, around the posterior rim of the talonid basin, and anteriorly along the labial base of the crown, connecting to the precingulid. M_2 has a low trigonid and its cusps are subequal in height. A heavy labial cingulid runs along the base of the crown from the precingulid to the hypoconid. The talonid of M_2 is proportionally longer than that of M_1. M^1 is triangular in outline with a wide protocone. The crown is rimmed by a cingulum on both its anterior and posterior edges. The pre- and postprotocingula do not connect around the base of the protocone. The paracone is taller than the metacone, but both cusps are lower and more rounded than in *Viverravus*. There are large, distinct para- and metaconules. The parastyle is large and hooked and the metastyle is small or absent. The stylar shelf is extremely narrow and has a low cingulum running its length. M^2 is smaller than M^1 and has a broad protocone. The paracone is taller than the metacone and there are small para- and metaconules. The postprotocrista does not extend labially along the posterior margin of the crown, nor does it connect around the base of the protocone to the preprotocrista.

Measurements of the posterior cheek teeth of *Didymictis leptomylus* are presented in Table 7.

Didymictis protenus (Cope,1874)

Fig. 15

Limnocyon protenus Cope, 1874, p. 602.

Didymictis protenus, Cope, 1875, p. 11; 1877, p. 123, plate 39, figs 1-9; 1883, p. 311, plate 25d, figs. 4 and 5. Matthew and Granger, 1915, p. 21.

Didymictis curtidens, Cope, 1882, p. 160. Cope, 1883, p. 313, plate 24d, fig. 10.

Didymictis protenus lysitensis, Matthew and Granger, 1915, p. 21, fig. 14.

Didymictis altidens lysitensis, Kelley and Wood, 1954, p. 348, fig. 6, E, F.

Didymictis protenus (in part), Bown, 1979, p. 93 (large variety). Davidson, 1987, p. 119.

Holotype.—USNM 1092, two dentaries with cheek teeth.

Type locality.—San Juan Basin, New Mexico. Probably Wa-5 or Wa-6 (Gingerich, personal communication).

Age and distribution.—Earliest through late Wasatchian (early Eocene) of western North America.

Definition.—An evolutionary species consisting of the series of ancestor-descendant populations between speciation (cladogenic) events that contains the holotype of *Didymictis protenus* (USNM 1092).

Diagnosis.—Differs from both *Didymictis proteus* and *D. leptomylus* in being significantly larger in all linear measurements and in having a smaller metastyle on M^1.

Referred specimens.—**Middle Sandcouleean**[Wa-1]: **SC-4**: UM 66736. **SC-160**: UM 68142. **SC-161**: UM 77485 and 80695. **SC-210**: UM 87421. **SC-211**: UM 69726. **SC-287**: UM 73770. **SC-316**: UM 101801. **Late Sandcouleean**[Wa-2]: **MP-20**: UM 87482. **MP-23**: UM 87663 and 87664. **MP-48**: UM 92122. **SC-54**: UM 67520. **SC-87**: UM 76524. **SC-88**: 86204. **Early Graybullian** [Wa-3]: **MP-138**: UM 93243. **MP-145**: UM 93471. **MP-147**: UM 93587. **MP-158**: UM 93885 and 93905. **MP-231**: UM 96278. **MP-272**: UM 99135. **SC-36**: UM 71701. **SC-213**: UM 71056. **SC-214**: UM 69885. **SC-225**: UM 71222. **SC-237**: UM 79019. **SC-310**: UM 86013. **Middle Graybullian** [Wa-4]: **MP-15**: UM 86919. **MP-123**: UM 92666, 94513, 94525, 94534, and 94539. **MP-142**: UM 93350 and 93357. **MP-167**: UM 99312. **MP-175**: UM 94360. **MP-177**: 94419. **MP-178**: UM 94446. **SC-255**: UM 74637, 80132, and 80133. **SC-265**: UM 87724. **SC-303**: UM 101840. **YM-421**: UM 64082, 64097, 64107, 64108, 64144, 64245, 64277, and 64283. **Late Graybullian** [Wa-5]: **GR-9**: UM 75290. **MP-62**: UM 91239. **MP-86**: UM 91808, 91821, 91905, 94544, and 91865. **MP-150**: UM 93692. **MP-151**: UM 93698. **MP-152**: UM 93725, 93746, and 93809. **MP-173**: UM 95019, 95023, and 95047. **MP-180**: UM 94577. **MP-257**: UM 97151. **SC-295**: UM 74014. **YM-320**: UM 64239. **YM-421**: UM 64287 and 64485. **YM-428**: UM 63985 and 64335. **Lysitean** [Wa-6]: **GR-14**: UM 75551. **MP-6**: UM 82418. **MP-41**: UM 96738. **MP-42**: UM 88293. **MP-59**: UM 91136, 97344, 97432. **MP-60**: UM 91495. **MP-66**: UM 91343. **MP-73**: UM 91447. **MP-76**: UM 91519 and 91558. **MP-90**: UM 92074. **MP-101**: UM 92189. **MP-102**: UM 92202. **YM-45**: UM 64199.

Description.—The dental formula of *Didymictis protenus* is I^3_3 C^1_1 P^4_4 M^2_2. It has a robust, deep jaw with two mental foramina, one below the diastema between P_1 and P_2 and the second between P_3 and P_4. Its coronoid process is high, but the masseteric fossa is not deep. The angular process is positioned above the axis of the ventral margin of the dentary. The mandibular symphysis, which is long and unfused, is oriented posteromedially. The mandibles, in articulation with each other at the symphysis, are constricted anteriorly, but flare laterally posterior to the symphysis. The snout, reciprocally, is medially constricted anterior to P_2, but the posterior part of the palatal margin flares laterally.

The lower incisors are small, crowded, and single-rooted. They form a straight, transverse line across the anterior margin of the lower jaw just medial to the anterior margin of the canine. No incisor crowns are preserved so their morphology remains unknown. The lower canine is robust and recurved with vertical striations covering its surface. P_1 is small and its roots are in a single alveolus. Its crown is not preserved in any specimens. P_2 is separated from P_1 by a short diastema with a single cusp situated anteriorly on the crown. P_3 is separated from P_2 by a short diastema, but its crown is more complex. It has three cusps: a tiny anterior accessory cusp, a large main cusp, and a smaller posterior accessory cusp. A cristid runs along the anteroposterior axis of the crown connecting the apices of all three cusps. A small notch is found between the base of the main cusp and the posterior accessory cusp. The base of the crown is partially ringed by a cingulid running from the posterior margin of the main cusp, around the posterior margin of the tooth, then anteriorly to the anterior accessory cusp. P_4 is the largest of the lower premolars and has four cusps. The smallest of these are the anterior and second posterior accessory cusps. The tallest is the main cusp. The base of the crown is almost completely ringed by a cingulid from the anterior margin of the main cusp on the lingual side, around the labial rim of the tooth, to the posterior margin of the main cusp, again on its lingual side. Like on P_3, a cristid runs along the anteroposterior axis of the tooth connecting the cusps and a notch is located between the main cusp and the first posterior accessory cusp. There is a small basin at the posterior end of the tooth, which is rimmed anteriorly by the main cusp, labially by the first posterior accessory cusp, and posterolingually by the basal cingulid.

M_1 is the largest tooth of the lower dentition. It has a high trigonid, on which the protoconid is the tallest cusp and the metaconid is the shortest. The metaconid and paraconid are relatively close together, giving the trigonid a closed appearance in lingual view. There

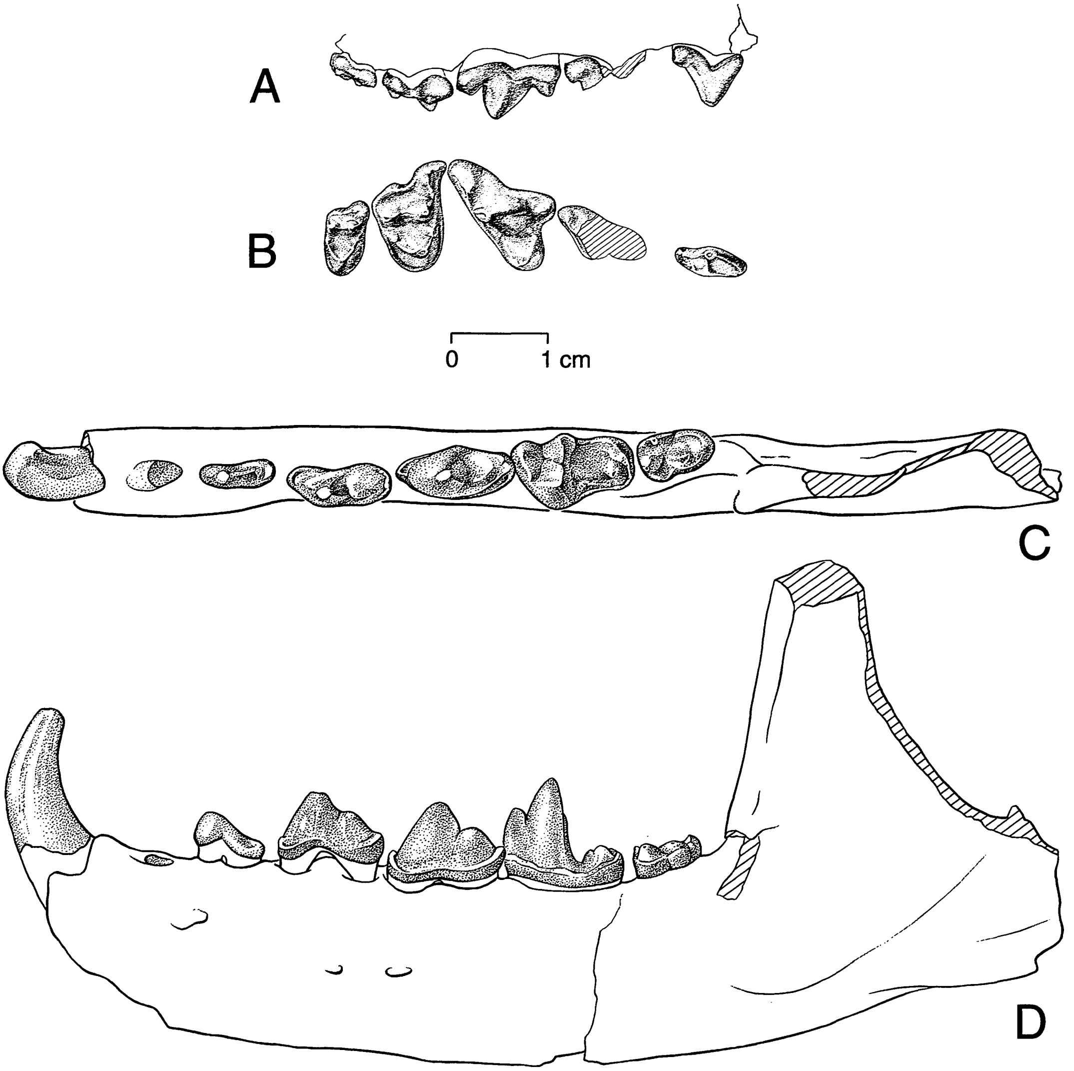


FIG. 15—Upper and lower dentitions of *Didymictis protenus* from the Wasatchian of the Clarks Fork basin: right maxilla fragment (UM 71056, SC-213) with P^2-M^2 in lateral (A) and occlusal (B) views, and left dentary (UM 64199, YM-45) with C_1-M_2 in occlusal (C) and lateral views (D).

is a distinct precingulid that ends at the base of the protoconid in some individuals, but is continuous with a basal cingulid rimming the labial base of the talonid. The talonid basin is large with an entoconid and hypoconid. In some individuals, a small hypoconulid can be distinguished from the entoconid. There is no cingulid on the lingual side of the tooth, but one runs from the posterior point of the talonid basin along its labial border to the base of the protoconid. M_2 is significantly smaller than M_1 and has a lower trigonid. The protoconid and paraconid, the largest cusps, are subequal in size and the metaconid is somewhat smaller. The talonid of M_2 is much larger than the trigonid. In some individuals, there are two main cusps: a hypoconulid and a hypoconid. In other individuals, there is also a distinct entoconid. A labial cingulid runs from the apex of the hypoconulid, around the labial base of the crown, and continues anteriorly as the precingulid.

TABLE 8—Summary of measurements of the upper and lower cheek teeth of *Didymictis protenus* from the Bighorn and Clarks Fork Basins, Wyoming. Specimens included here are from the early (Wa-1) through late Wasatchian (Wa-6). Change in the size of the species through this time contributes to its variability (see Figure 8). Because of this, all statistics are tabulated by faunal zone. All measurements in millimeters.

Tooth position	N	Observed range	Mean	Standard deviation	Coefficient of variation
			Wa-1		
Upper dentition					
P^4 L	2	11.06 -11.60	—	—	—
W	2	9.97 -12.37	—	—	—
M^1 L	3	7.81 - 8.19	7.99	—	—
W	3	10.68 -11.07	10.86	—	—
M^2 L	2	4.98 - 5.06	—	—	—
W	2	7.63 - 7.65	—	—	—
Lower dentition					
P_4 L	2	10.75 -11.46	—	—	—
W	2	4.37 - 4.80	—	—	—
M_1 L	3	11.46 -13.34	12.13	—	—
W	3	6.44 - 7.55	7.02	—	—
M_2 L	3	8.05 - 9.62	8.64	—	—
W	3	4.33 - 5.86	4.86	—	—
			Wa-2		
Upper dentition					
P^4 L	3	8.74 -10.36	9.76	—	—
W	3	10.00 -12.34	11.02	—	—
M^1 L	2	8.44 - 9.11	—	—	—
W	2	11.42 -11.95	—	—	—
M^2 L	2	4.20 - 4.26	—	—	—
W	2	7.74 - 7.90	—	—	—
Lower dentition					
M_1 L	2	10.13 -10.30	—	—	—
W	2	6.14 - 6.18	—	—	—
M_2 L	2	6.47 - 7.80	—	—	—
W	2	4.10 - 4.60	—	—	—
			Wa-3		
Upper dentition					
P^4 L	2	10.77 -11.97	—	—	—
W	2	12.47 -12.47	—	—	—
M^1 L	5	6.62 - 8.99	7.58	0.9001	11.88
W	5	9.91 -12.89	10.94	1.1594	10.60
M^2 L	3	4.65 - 4.75	4.69	—	—
W	3	7.54 - 7.80	7.68	—	—
Lower dentition					
P_4 L	1	11.36	—	—	—
W	1	5.31	—	—	—
M_1 L	6	9.36 -12.12	10.14	1.0221	10.08
W	6	5.63 - 7.47	6.12	0.7010	11.46
M_2 L	2	7.02 - 7.45	—	—	—
W	3	3.98 - 4.56	4.32	—	—
			Wa-4		
Upper dentition					
P^4 L	2	10.88 -11.20	—	—	—
W	2	10.22 -10.54	—	—	—
M^1 L	3	6.88 - 8.16	7.55	—	—
W	3	10.45 -11.21	10.87	—	—
M^2 L	1	3.97	—	—	—
W	1	7.81	—	—	—

Lower dentition					
P_4 L	11	9.22 -11.79	10.66	0.6990	6.56
W	11	3.59 - 4.85	4.43	0.4514	10.41
M_1 L	14	10.14 -11.82	10.69	0.4722	4.42
W	15	5.80 - 7.16	6.46	0.4304	6.66
M_2 L	11	6.36 - 7.84	7.26	0.4728	6.51
W	11	3.83 - 4.74	4.16	0.2888	6.94
		Wa-5			
Upper dentition					
P^4 L	4	10.86 -13.08	11.53	1.0453	9.07
W	4	11.20 -13.59	12.46	1.2643	10.14
M^1 L	6	8.07 -10.16	8.77	0.7208	8.22
W	7	10.98 -13.00	11.95	0.7516	6.29
M^2 L	4	4.17 - 4.54	4.41	0.1700	3.86
W	4	7.43 - 8.31	7.84	0.3668	4.68
Lower dentition					
P_4 L	5	10.28 -10.73	10.51	0.2115	2.01
W	5	4.08 - 4.75	4.35	0.3064	7.05
M_1 L	12	9.82 -12.44	11.38	0.8756	7.70
W	12	6.02 - 7.69	6.76	0.5378	7.95
M_2 L	7	7.41 - 8.35	7.94	0.3556	4.48
W	7	4.30 - 4.76	4.54	0.1585	3.49
		Wa-6			
Upper dentition					
P^4 L	4	11.24 -13.77	12.19	1.0978	9.01
W	4	11.92 -14.82	13.16	1.2298	9.35
M^1 L	3	9.37 - 9.75	9.52	—	—
W	3	13.12 -14.36	13.69	—	—
M^2 L	1	5.26	—	—	—
W	1	8.81	—	—	—
Lower dentition					
P_4 L	8	11.60 -13.20	12.59	0.5102	4.05
W	8	4.97 - 5.98	5.31	0.3638	6.85
M_1 L	7	12.43 -15.62	13.53	1.0447	7.82
W	8	7.07 - 8.40	7.64	0.3912	5.12
M_2 L	3	7.68 - 8.48	8.15	—	—
W	3	4.57 - 5.11	4.86	—	—
		All faunal zones			
Upper dentition					
P^4 L	17	8.74 -13.77	11.27	1.1191	9.93
W	17	9.97 -14.82	11.99	1.4041	11.71
M^1 L	22	6.62 -10.16	8.33	0.9226	11.08
W	23	9.91 -14.36	11.65	1.1558	9.92
M^2 L	13	3.97 - 5.26	4.57	0.3782	8.27
W	13	7.43 - 8.81	7.84	0.3594	4.58
Lower dentition					
P_4 L	27	9.22 -13.20	11.26	1.0393	9.23
W	27	3.59 - 5.98	4.68	0.5850	12.49
M_1 L	44	9.36 -15.62	11.30	1.2989	11.49
W	46	5.63 - 8.40	6.72	0.6782	10.09
M_2 L	28	6.36 - 9.62	7.66	0.6837	8.92
W	29	3.83 - 5.86	4.42	0.4214	9.52

P^1 is a small, two-rooted tooth with a single cusp on the crown. The cusp is located over the anterior root. P^2 is larger and, in addition to the main cusp, possesses a small posterior accessory cusp. The tooth is two rooted and the main cusp is located mid-length between the roots. P^3 is separated from P^2 by a short diastema and is slightly larger than P^2. It has a distinct lingual cingulum making it proportionally wider than either P^1 or P^2. It has a tall, rounded main cusp as well as a tiny anterior accessory cusp and a larger posterior accessory cusp. There is a small carnassial notch between the main cusp and the posterior accessory cusp. The entire circumference of the crown is rimmed by a cingulum. P^4 is both larger and more complex than P^3. It has a large paracone, a very distinct, anteriorly placed parastyle cusp, a large protocone, and a large metastyle blade with a carnassial notch between the metastyle and the paracone. A cingulum rims the entire circumference of the tooth crown.

M^1 is approximately the same size as P^4. It has a large, hooked parastyle, but the metastyle is small or absent. The paracone is the tallest trigon cusp, followed by the protocone, which is very broad anteroposteriorly, and the shortest cusp is the metacone. The paraconule and metaconule are small and conical. The entire tooth crown is rimmed by a basal cingulum incorporating both the pre- and postprotocingula. M^2 is significantly smaller than M^1. Its parastyle is relatively large, although not as large as that of M^1, and the metastyle is small or absent. The protocone is the largest cusp and the metacone the smallest. The metaconule and paraconule are small and conical, as in M^1. The crown is almost completely rimmed by a basal cingulum, although in some individuals it is not connected across the lingual base of the protocone between the two protocingula.

Measurements of the posterior cheek teeth of *Didymictis protenus* are presented in Table 8.

CONCLUSIONS

Many debates within cladistics in the past decade have centered on fossils and their utility in reconstructing phylogeny. These include papers by Schaeffer et al. (1972), who questioned the methodology used in ancestor recognition, and Patterson (1981), who went farther by saying that fossil data have no bearing on our understanding of the relationships of living taxa. The last of these was repudiated by Gauthier et al. (1988), who showed that it was not how complete a taxon is, but the combination of characters that it possesses that determine its informativeness in cladistic analysis. Gauthier et al. demonstrated that a cladogram based solely on recent taxa could be overturned by the inclusion of fossil taxa in a parsimony-based analysis.

The first debate—that ancestors may be unknowable—has remained more controversial until recently. In the past few years, many papers have explored the efficacy of fossil and stratigraphic data to complement and extend purely morphological data in the study of phylogeny (*e.g.*, Fisher, 1991, 1992, 1994; Norell, 1992, 1993; Thewissen, 1992; Archibald, 1994; Erwin and Anstey, 1995; Wagner, 1995). Objections to the concept of direct ancestry from within more rigid cladistic circles have included the assertion that the discovery of direct ancestors should not be a major goal of systematics when the likelihood of recovering them is so low. This objection is a red herring—none of the authors cited above have argued that the goal of phylogenetic analysis is the identification of direct ancestors. Their point was, and the point of this paper is, that the possibility exists for fossil taxa to be direct ancestors—in fact that probability may be quite high (Foote, 1996). Any methodology that deals with historical data should be capable of scientifically assessing this possibility—there should be no *a priori* assertions as to whether a taxon is or is not an ancestor.

In this paper, I have used stratocladistics (Fisher, 1991, 1992, 1994) as an approach for proposing and testing hypotheses of ancestry. It is much easier to falsify an hypothesis in a scientific framework than to prove it. For this reason, Popper (1959) argued that a true scientific hypothesis was one that could be overturned by the application of new data or experiments. It is possible to falsify an hypothesis of ancestry, but it is almost impossible to prove that a taxon was an ancestor (Engelmann and Wiley, 1977). A methodology that presumes that a taxon is not an ancestor until proven otherwise runs the risk of being unscientific—the assertion that ancestry is unknowable and that fossil taxa can only be considered as terminal taxa in a cladistic analysis is such a methodology. Once an hypothesis of ancestry has been framed, a variety of data, including both cladistic character analysis and stratigraphic analysis, are capable of overturning it. Such an approach will bolster the study of phylogeny.

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APPENDIX 1: CHARACTER DESCRIPTIONS

Morphological characters used in the phylogenetic analysis. Character states for each taxon are listed in Appendix 2.

1. $M^3/_3$ present (0) or absent (1).
2. Canine surface with a few distinct ridges along its length (0), smooth (1), or with many minute grooves (2).
3. Protocone on P^3 large with cusp (0), reduced without cusp (1), or absent (2).
4. P^4 about the same length as M^1 (0) or proportionally much longer (1).
5. Basal cingulum on P^4 present only on labial side of the tooth (0), also present along the posterior base of the protocone (1), or also present on both the anterior and posterior of the protocone (2).
6. Parastyle on P^4 large and anteriorly positioned (0), slightly reduced (1), or quite reduced (2).
7. Deep vertical notch in the metastyle of P^4 (0) or with a shallow notch (1).
8. Protocone of P^4 large and projecting somewhat anteriorly (0) or projecting far anteriorly such that it is close to the parastyle (1).
9. Metastyle on M^1 long with a small carnassial notch (0), small with no carnassial notch (1), or absent (2).
10. Metaconules on M^1 present and winged (0), present and conical (1), or absent (2).
11. Preprotocingulum absent on M^1 (0), present, but not connected to the postprotocingulum (1), or connected to the postprotocingulum across the base of the protocone (2).
12. Postprotocingulum absent on M^1 (0), present (1), posteriorly expanded into a pre-hypocone lobe (2), expanded with a small hypocone cusp (3).

13. Metacone on M^1 subequal in height to the paracone (0), slightly smaller than paracone (1), considerably smaller than paracone (2).
14. Metacone and paracone of M^1 trenchant and connected at the base (0), conical and not connected at the base (1).
15. Parastyle on M^1 large and hooked with a large parastyle cusp (0) or smaller with no cusp (1).
16. Lower canine without cristid (0) or with cristid running from its tip to its base on the posterior side (1).
17. P_1 double-rooted (0), double-rooted with roots in a single alveolus (1), or single-rooted (2).
18. P_3 with two posterior accessory cusps (0) or with only a single, small posterior accessory cusp (1).
19. P_3 roughly equal in length to P_4 (0) or considerably reduced in length (1).
20. Main cusp of P_3 slightly shorter than that of P_4 (0), subequal in height (1), or much shorter (2).
21. Basal labial cingulid on P_4 absent (0), present, but light and not continuous anteroposteriorly (1), heavy and running along the entire labial face of the tooth (2).
22. Second posterior accessory cusp on P_4 large with notch between it and the first posterior accessory cusp (0), small with notch (1), small without notch (2), or absent (3).
23. Anterior accessory cusp on P_4 present but small and conical (0), large and trenchant (1), or absent (2).
24. Margin of P_4 labial to the main cusp narrow (0) or absent (1).
25. First posterior accessory cusp positioned at a medium height on the posterior flank of main cusp on P_4 (0), at a high on the main cusp (1), or low on the main cusp (2).
26. Notches between the main and posterior accessory cusps on P_4 present (0) or absent (1).
27. Basin on posterior of P_4 large and rimmed by a cingulid (0) or small and rimmed by a cingulid (1).
28. Position of metaconid on M_1 positioned lateral to the posterior of the protoconid (0), positioned far posteriorly giving the trigonid a very open appearance in lingual view (1), or positioned anteriorly, giving the trigonid a closed appearance (2).
29. Cristid obliqua on M_1 angled toward the midline of the tooth (0) or parallel to the midline (1).
30. Talonid cusps high and basin deeply sloping towards the talonid notch (0) or talonid cusps lower and basin floor relatively horizontal with the talonid notch closed by the entocristid (1).
31. Hypoconulid on M_1 present (0), reduced (1), or absent (2).
32. Basal cingulid of M_1 absent (0), rimming lingual face of the talonid (1), or rimming the entire labial face of the crown (2).
33. Talonid about the same length as the trigonid on M_1 (0), slightly shorter (1), or considerably shorter (2).
34. Talonid narrower than the trigonid of M_1 (0) or about the same width (1).
35. Paraconid and metaconid on M_2 subequal in height (0) or paraconid shortest cusp and positioned far anteriorly (1).
36. Trigonid on M_2 very tall (0), short yet taller than talonid (1), or about the same height as talonid (2).
37. Talonid about the same length as the trigonid on M_2 (0), longer than trigonid (1), or much longer than trigonid (2).
38. M_2 talonid much narrower than the trigonid (0) or subequal in width (1).
39. Basal cingulid on M_2 absent (0), present on the labial face of the talonid (1), or completely rimming the labial face of the crown (2).

APPENDIX 2: CHARACTER MATRIX

Character states used in the phylogenetic analysis. Characters 1 through 39 are morphological characters (described in Appendix 1). The primitive state for viverravids is represented by a zero ("0") and more derived states by the numerals 1 through 3. Character 40 is a stratigraphic character with 14 states represented by the numerals 0 through 9 and the letters A through D. State 0 is the oldest (late Torrejonian) and state D is the youngest (Wa-6).

	Character number							
Taxon	1-5	6-10	11-15	16-20	21-25	26-30	31-35	36-40
Outgroup	00000	00000	00000	00000	00000	00000	00000	00000
Protictis haydenianus (To)	10001	00010	11110	02110	10010	01000	00100	11000
Protictis agastor (Ti-3)	1??01	00010	21100	?????	?????	??200	01000	11022
Protictis paralus (Ti-3)	11???	?????	?????	00?0?	10010	00000	00100	11002
Viverravus laytoni (Cf-2)	11???	???12	11110	1?0??	?????	??000	01100	11005
Viverravus politus (Cf-1)	1????	?????	?????	?????	?????	??100	0120?	????4
Viverravus politus (Cf-2)	1????	?????	?????	12112	10110	01100	01201	11005
Viverravus politus (Wa-1)	1?111	21112	11110	?2112	10110	01100	01201	11008
Viverravus politus (Wa-4)	1??11	21112	11210	?????	?????	?????	?????	????B
Viverravus acutus (Cf-3)	1????	?????	?????	?????	11110	00000	01100	11006
Viverravus acutus (Wa-1)	1??01	01012	12110	?????	12110	00000	01100	11008
Viverravus acutus (Wa-2)	1?201	01012	12110	?0000	12110	00000	01100	11009
Viverravus acutus (Wa-3)	1?201	11022	12110	?0000	12110	00000	01101	1100A
Viverravus acutus (Wa-4)	1?201	11022	12110	?0000	12110	00000	01101	1100B
Viverravus acutus (Wa-5)	1????	?????	?????	??000	12110	00000	01101	1100C
Viverravus acutus (Wa-6)	1??01	11122	12110	?0000	12110	00000	01101	1100D
Viverravus rosei (Cf-3)	1?20?	01?12	11110	?????	11111	0???0	0110?	????6
Viverravus rosei (Wa-1)	1????	?1???	?????	??00?	11111	00000	0110?	????8
Viverravus rosei (Wa-2)	1????	?????	?????	??001	11111	00000	0110?	????9
Viverravus rosei (Wa-3)	1????	?????	?????	?????	11111	00000	0110?	????A
Didymictis proteus (Ti-5)	10?0?	00010	11100	10000	20010	00201	12000	21023
Didymictis proteus (Cf-2)	10102	00020	21110	10001	20112	01211	12010	22125
Didymictis proteus (Cf-3)	1?102	00020	21210	?0001	20112	01211	12010	22126
Didymictis proteus (Wa-0)	10102	00020	21210	11001	20112	01211	12010	22127
Didymictis leptomylus (Wa-1)	10???	???20	21210	11001	20112	01211	12010	22128
Didymictis leptomylus (Wa-2)	1????	?????	?????	??001	20112	01211	22010	22129
Didymictis protenus (Wa-1)	1??02	00021	21210	?1001	23112	01211	22010	22128
Didymictis protenus (Wa-2)	1?102	00021	21210	?????	23112	01211	22010	22129
Didymictis protenus (Wa-3)	12102	00021	21210	1?001	23112	01211	22010	2212A
Didymictis protenus (Wa-4)	12102	00021	21210	11001	23112	01211	22010	2212B
Didymictis protenus (Wa-5)	12?00	00021	21210	11001	23112	01211	22010	2212C
Didymictis protenus (Wa-6)	12?00	00021	21210	11001	23112	01211	22010	2212D