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Phylogeny of Early Tertiary Carnivora, With a Description of a New Species of *Protictis* From the Middle Eocene of Northwestern Wyoming

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ABSTRACT

Since Cope erected the Miacidae in 1880, all early Tertiary carnivorans have generally been grouped in this family because of their overall primitive morphology. A historical review of the classifications and definitions of the Miacidae is provided. Discovery of a new subgenus of *Protictis* from the Uintan (mid Eocene) of northwestern Wyoming led to a reevaluation of the phylogeny of the Carnivora. The Miacidae (Miacidae), as previously constructed, is a paraphyletic assemblage of all the early Tertiary Carnivora. Phylogenetic analysis of the distribution of cranial, dental, and postcranial morphology indicates that the bipartite division recognized in living Carnivora may be traced to the earliest Tertiary representatives of this order. Most taxa previously included in the "Viverravinae" ("Miacidae") are members of the Feliformia and those placed in the "Miacinae" ("Miacidae") are Caniformia. Diagnoses and discussions are provided

for the suprageneric taxa Carnivora, Feliformia, Caniformia, Didymictidae (Didymictida) (new), Aeluroida (new), Feloida, and Viverravidae. *Protictis*, including the subgenera *P. (Protictis)*, *P. (Bryanictis)*, and *P. (Protictoides)* (new), is diagnosed and discussed. *Simpsonictis* is considered a valid genus and is allied with *Viverravus* in the Viverravidae (Aeluroida, Feliformia). *Palaeogale* is removed from the Mustelidae (Caniformia) and is considered a close relative of the Viverravidae. *Ictidopappus* is placed *incertae sedis* within the Aeluroida. "*Plesiomiaceis*" and *Quercygale*, which were previously considered members of the "Viverravinae," are considered members of the Caniformia. The sabretoothed "paleofelid" *Nimravidae* are excluded from the Feloida (Aeluroida, Feliformia) and are included instead within the Caniformia. A summary of the proposed phylogeny and a classification of the Carnivora are presented.

INTRODUCTION

Carnivorans have been represented in most collections of early Tertiary faunas

since the nineteenth century. Much valuable descriptive and interpretive work has been

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published on the carnivorans from these faunas in the past, although little has been written recently on the phyletic relationships of these animals. While many investigators have pursued intensive studies of the interrelationships of the living Carnivora, the critical Paleocene and Eocene Carnivora have remained largely ignored.

There is a pressing need for a critical review of the paraphyletically constructed family Miacidae. Since Cope established the Miacidae, this family has been considered a basal stock of primitive Carnivora. Regrettably, most workers have justified this practice by stressing that most of the early Tertiary forms lack the diagnostic features of the later, more advanced carnivorans. In general, the grouping of all primitive carnivorans has greatly hindered the determination of the specific interrelationships of the major carnivoran groups. In spite of this, a few attempts have been made to include miacid genera in the analysis and arrangement of carnivoran lineages (Wortman and Matthew, 1899; Wortman, 1901; Gregory and Hellman, 1939), but such efforts have not been generally accepted.

Tedford (1976) presented the first attempt at distinguishing the major carnivoran clades. Through an analysis of derived character states in the Carnivora he proposed a testable hypothesis of relationships for many groups of living and fossil carnivorans. This phylogeny of the Carnivora represents an important beginning in the advancement of our understanding of the evolutionary history of this group. Tedford's brief discussion of the relationships of Simpson's Miacoidea emphasizes the lack of knowledge of the distribution of derived characters within the Miacidae and the essential need for an analysis of the phylogenetic relationships of the miacid genera with other Carnivora: "The fact that very few miacoids have been identified as phyletically related to members of the modern superfamilies only increases the isolation of the archaic and modern carnivore families This represents one of the largest gaps in our knowledge of the phylogeny of the Carnivora" (Tedford, 1976, p. 364).

Such a gap exists partly because of the

predominance of primitive morphologies in the Miacidae, but it is also a result of the failure of most previous workers to distinguish advanced characters that might ally various miacid taxa to later Carnivora. This paper attempts to decrease the gap in our understanding of carnivoran phylogeny. The Miacidae are no longer treated as a miscellaneous collection of primitive, early Tertiary Carnivora. Instead we apply a phylogenetic methodology to an analysis of "miacid" genera (particularly the "Viverravinae") in an attempt to determine the relationship between these forms and the later, advanced carnivorans. The Miacidae were not a closely allied group that formed, in its entirety, the primordial stock for all later Carnivora. The differentiation into the two distinct lineages (Caniformia and Feliformia) recognized in living carnivorans, occurred early in carnivoran phylogeny and is definitively reflected in the phylogenetic alliances of the early Tertiary Miacidae.

The early Tertiary Carnivora have generally been classified in a single horizontal group, the Miacidae, although many workers have recognized that various "miacids" are more closely related, phylogenetically, to other carnivoran taxa than to each other (see especially Matthew, 1909, p. 354). This study analyzes the phylogenetic relationships of the early Tertiary carnivorans to other carnivorans in greater detail than did prior studies, concentrating particularly on the distribution of shared derived dental features in these taxa. The results of this phylogenetic analysis are then used to construct a cladistic classification of the Carnivora. The inclusion of the early Tertiary Carnivora in a detailed phylogenetic analysis and vertical classification of the entire Carnivora is very different from the treatment the "miacids" have received in earlier studies. We believe that this is an important step in discerning the precise relationship of the archaic to the living carnivorans. In any study an important distinction must be made between hypotheses of phylogeny and methods of classification. We propose here a testable hypothesis of phylogenetic relationships for the Carnivora, and then use this phylogeny

to construct a vertical classification that reflects and is consistent with the proposed phylogeny.

The impetus for the present study came from the discovery of new carnivoran material from the Uintan Tepee Trail Formation of northwestern Wyoming (see McKenna, 1980; MacFadden, 1980). An attempt to determine the precise taxonomic affinities of these dental specimens immediately produced some interesting biostratigraphic and systematic results. All previous carnivorans from the North American Uintan had been referred to the Miacinae, as the Viverravinae (except possibly *Plesiomiakis*, see the later discussion of this genus) appeared to reach extinction in the Bridgerian. However, even the limited material available from the Tepee Trail Formation indicated that this form was truly a Uintan "viverravine," whose closest relative was the Torrejonian genus *Protictis*. Furthermore, it became obvious that since the "Miacidae" was so clearly separable into two morphologically distinct subfamilies (recognizable even on the basis of only limited dental material), the family was most likely a paraphyletic assemblage of generally primitive carnivoran species. An analysis of the character distributions and the construction of a hypothesis of relationships for the "Miacidae" (and the "Viverravinae," in particular) followed in an attempt to determine whether these were truly monophyletic taxa. The possible relationship between various "miacids" and more advanced Carnivora was also investigated at that time. This paper represents the conclusions drawn during various stages of analysis of the series of problems that arose from the initial attempt to identify and to determine the phylogenetic relationships of the Tepee Trail carnivoran.

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ABBREVIATIONS

AMNH, Department of Vertebrate Paleontology, American Museum of Natural History, New York.

USNM, United States National Museum, Smithsonian Institution, Washington, D.C.

AC, Pratt Museum, Amherst College, Amherst, Massachusetts.

TERMINOLOGY

The dental terminology used in this paper is shown in figure 1. Additional terminology not on this figure follows the usage of Van Valen (1966), MacIntyre (1966) and Szalay (1969). We have chosen not to use molar terminology for P_4 morphology because we do not believe that there is a simple homology between the features of the lower molars and premolars in the Carnivora. Because of the uncertainty of developmental origins and confusion about the primitive "molariform" or "premolariform" nature of the eutherian P_4 , we prefer to use a descriptive premolar terminology.

MEASUREMENTS

An EPOI "Shopscope" and an IKL "Microde" Precision Digital Positioner accurate to 0.001 mm. were used to make measurements and are recorded to 0.01 mm. Measurements follow the orientations described by MacIntyre (1966, p. 126).

HISTORICAL REVIEW OF MIACID CLASSIFICATION

Flower (1869, 1883) proposed the division of the living Carnivora into the Arctoidea, Cynoidea, and Aeluroidea. This arrangement has been followed, in one modified form or

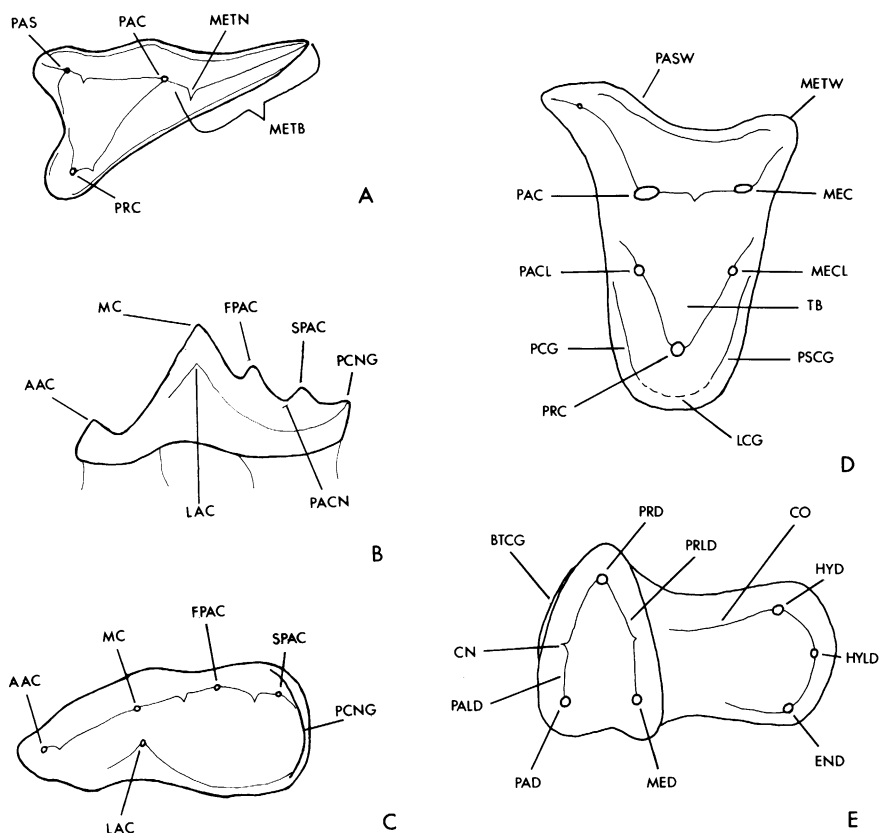


FIG. 1. Dental terminology. Diagrammatic representation of carnivoran right P_4^4 and M_1^1 , indicating the descriptive terminology used in this paper. A) Occlusal view of P_4^4 , B) lingual view of P_4^4 , C) occlusal view of P_4^4 , D) occlusal view of M_1^1 , E) occlusal view of M_1^1 . AAC—anterior accessory cusp; BTCG—basal trigonid cingulum; CN—carnassial notch; CO—cristid obliqua; END—entoconid; FPAC—first posterior accessory cusp; HYD—hypoconid; HYLD—hypoconulid; LAC—lingual accessory cusp; LCG—lingual cingulum; MC—main cusp; MECL—metaconule; MED—metaconid; METB—metastyle blade; METN—metastyle notch; METW—metastyle wing; PAC—paracone; PACL—paraconule; PACN—posterior accessory cusp notch; PAD—paraconid; PALD—paralophid; PAS—parastyle; PASW—parastyle wing; PCG—precingulum; PCNG—posterior cingulum; PRC—protocone; PSCG—postcingulum; PRD—protoconid; PRLD—protolophid; SPAC—second posterior accessory cusp; TB—talonid basin. Anterior toward left of page. Buccal toward top of page in A, C, D and E.

another, by most subsequent workers. Simpson (1945) provided the most recent comprehensive review of the various classifications proposed for living carnivorans.³ Tedford (1976), in his discussion of pinnipeds, con-

sidered the morphology and systematics of the living, and some fossil, Carnivora in a phylogenetic framework. In that study Tedford reviewed previous morphological and classificatory studies of Carnivora and proposed a bipartite division into Caniformia and Feliformia.

Authors of previous studies of fossil Carnivora (Matthew, 1901a, 1909, 1915; Simpson, 1937; Hough, 1948, 1953; MacIntyre,

³ We follow Van Valen's (1969) suggestion that, in order to avoid terminological ambiguity, the common term "carnivoran" be used to distinguish members of the order Carnivora from other carnivorous mammals.

1966) have invariably considered all Paleocene and Eocene carnivoran genera as members of the Miacidae. The Miacidae were erected by Cope in 1880a (p. 78) basically as a grouping of all the primitive Carnivora, and included the genera *Miacis* and *Didymictis* (see table 1 for a detailed summary of the classifications discussed in this paper). Cope believed in a horizontal scheme of classification in which taxa of a generally primitive nature were grouped with even more primitive "stem-groups." Even if members of a given taxon shared a few derived characters (synapomorphies) with, and were clearly related phyletically to, more advanced forms, they were classified with more primitive taxa because of greater overall primitiveness. The Miacidae were therefore included by Cope (1880a, 1883) within the paraphyletic Creodonta, which also included the Arctocyoniidae, Leptictidae, Oxyaenidae, Amblyctoniidae, and Mesonychidae.

Trouessart's (1885) catalogue of carnivores listed the Miacidae within Cope's (1880a) Creodonta, and added a new subfamily Miacinae. This first attempt at dividing the Miacidae below the familial level did not include a taxonomic diagnosis or discussion, nor was there another taxon proposed of equivalent rank to the Miacinae.

Flower and Lydekker (1891) divided the order Carnivora into the three suborders Carnivora Vera, Pinnipedia, and Creodonta.

Wortman and Matthew (1899) considered the phyletic relationships of living carnivorans and determined that the ancestry of the Canidae and Viverridae could be traced directly back to the Eocene "Creodonta." They synonymized the genotype of *Miacis* Cope with *Vulpavus* Marsh, included most of the species of *Miacis* under *Uintacyon* Leidy, and concluded that *Uintacyon* was ancestral to and should be included within the Canidae. Wortman and Matthew also proposed a new family Viverravidae to include the species previously assigned to *Didymictis* Cope, which they synonymized with *Viverravus* Marsh. By including *Uintacyon* (*Miacis*) in the Canidae and placing *Viverravus* (*Didymictis*) in a new family, these workers effectively abandoned the

family Miacidae. The Viverravidae were considered members of a lineage distinct from the Canidae, and assumed to be ancestral to the living Viverridae, as proposed much earlier by Wortman (1886) and Flower and Lydekker (1891).

Wortman's (1901) study of the Eocene Mammalia from the Yale Peabody Museum Marsh Collection expanded on ideas presented jointly with Matthew in 1899. Wortman proposed and defined the carnivoran suborder Carnassidentia, equivalent to the suborder Carnivora Vera of Flower and Lydekker (1891). Wortman emphasized the importance of dental characters in defining carnivoran groups, and realized that the unfused state of carpal elements was primitive, that it may occur in many different lineages, and that its occurrence was therefore not indicative of close phyletic relationship. Together with the Creodonta and Pinnipedia, the Carnassidentia formed a tripartite division of the Carnivora. Wortman (1901) further considered the relationships of the Eocene Canidae and Viverravidae; more rigorously defined the Viverravidae; named *Oödetes* as an Eocene viverravid; distinguished the Viverravidae from the contemporary Canidae, the successor Viverridae, and the Mustelidae; and criticized Matthew's (1901a) arrangement of the Creodonta.

Matthew's (1901a, p. 59) classification of the Creodonta followed Schlosser's (1888) subdivision of the group into Creodonta Primitiva (including Oxyclaenidae), Creodonta Adaptiva (including Palaeonictidae, Viverravidae, and Arctocyoniidae), and Creodonta Inadaptiva (including Oxyaenidae, Hyaenodontidae, and Mesonychidae). He included the Viverravidae in the Creodonta Adaptiva, and tentatively excluded *Vulpavus* and *Uintacyon* from the Viverravidae and Creodonta by retaining them in the Canidae, but he also suggested that *Vulpavus* and *Uintacyon* might later be placed in the Creodonta if they proved to have the creodont tarsus.

Matthew (1909), in his extensive monograph on the fossils of the Bridger Basin Eocene, continued to utilize Schlosser's (1888) and his own (1901a) concept of Creodont

[illegible]

donta Adaptiva and Inadaptiva in his subdivision of the Creodonta into the Eucrodi (=Adaptiva; including Arctocyoniidae and Miacidae), Pseudocrodi and Acreodi (together = Inadaptiva; including Hyaenodontidae, Oxyaenidae, Mesonychidae, and Oxyclaenidae). Although he retained the Eucrodi within the Creodonta, Matthew subsequently (1909, pp. 330, 339–340) stated that the Miacidae, only, were definitely ancestral to later Fissipedia. Furthermore, Matthew (1909, p. 354) suggested that the Viverravinae and Miacinae may have been ancestral to the Aeluroidea and Arctoidea, respectively, although they remained grouped in the same family as an expression of their recent common ancestry and shared primitive morphological structure.

Although Matthew (1901a, 1909) followed Cope's classification of the Miacidae in the Creodonta, he dealt more explicitly with the philosophical considerations of horizontal, gradal classifications, as is seen in this passage: "It will be observed that the definition of the suborder Creodonta is in accord with the general views of its author upon its classification and phylogeny, according to which the suborder represented a structural group, defined by the possession of certain common characters indicative of relationship. The alternate theory of classification, that an order, family or other division represents a phylogenetic line, including animals often of widely different structure but which in the opinion of the classifier are genetically connected, will of course involve a radical change in our conception of the Creodonta, regarding the inadaptable forms as pseudo-Carnivora, and transferring the adaptable group to the Fissipedia" (Matthew, 1909, p. 320).

Matthew (1909) also resurrected the Miacidae as a diagnosable family of primitive, early Tertiary carnivorans classified within the Eucrodi of the Creodonta. *Uintacyon* and *Vulpavus* were removed from the Canidae and were considered members of the Miacidae. Matthew (1909) proposed and diagnosed the two subfamilies Viverravinae and Miacinae, for the Viverravidae and the Eocene "Canidae," respectively. The

subfamily designation for the Viverravinae was new, whereas the use of Miacinae was a resurrection of Trouessart's (1885) taxon for a different and more restricted group of miacids. This arrangement brought together the primitive relatives of the later carnivorans, but retained, somewhat, the concept of an early split of the living forms into two distinct lineages. Matthew considered invalid the synonymies of *Didymictis* with *Viverravus* and *Miacis* with *Vulpavus* (as proposed by Wortman and Matthew, 1899, and followed by Wortman and Matthew 1901a).

In his 1915 revision of the fauna of the Wasatch and Wind River Eocene, Matthew keyed the families of Creodonta (p. 5), the genera of Miacidae (p. 18) and the species of *Didymictis* (p. 20), and considered the phyletic affinities and stratigraphic distributions of the Miacidae.

The monograph by Matthew on the Paleocene of the San Juan Basin, published posthumously in 1937, included further discussion and definition of the Creodonta, Miacidae, and *Didymictis*. The classification and ideas presented there differed little from those elaborated in 1909 and 1915, although Matthew did propose a new subgenus *Proctictis* for *Didymictis haydenianus*.

The arrangements presented in the 1909, 1915, and 1937 papers were more consistent with Matthew's gradistic philosophy than was the one proposed in 1901a. The two classifications of Matthew and Wortman are strikingly different, and emphasize the methodological and philosophical split between the two. Matthew's classification was essentially horizontal and stressed the retention of a majority of primitive characters by the Viverravidae, and possibly the recent common ancestry between this family and the remainder of the Creodonta, even though he retained the Eocene genera *Uintacyon* and *Vulpavus* within the Canidae. Wortman's scheme was more vertical in emphasis; he included the Viverravidae with more advanced carnivorans on the basis of shared derived dental morphology, in an attempt to distinguish the course of phyletic diversification. The inclusion of the primitive *Uintacyon* and *Vulpavus* in the more advanced

Canidae was more consistent with Wortman's methodology than with Matthew's.

Simpson described a new viverravine genus, *Ictidopappus*, and two new species of *Didymictis*, *D. tenuis* and *D. microlestes*, from the Fort Union Paleocene of Montana in 1935. Simpson later (1937) considered the relationships of these species, as well as other Viverravinae, and provided diagnoses for the Viverravinae, *Didymictis*, and *Ictidopappus*. His arrangement of the Viverravinae followed that of Matthew (1909), whereas his discussion of *Ictidopappus* suggested that this genus might be ancestral to *Viverravus* or that *Viverravus* might be an offshoot of *Didymictis*.

The concept of the Miacidae had thus remained as espoused by Matthew (1909, 1915, 1937) and followed by Simpson (1935, 1937), until 1939 when Gregory and Hellman published a study on the evolution and classification of the Viverridae. That paper presented a radical departure from previous classifications and notions of relationships. Gregory and Hellman adapted Matthew's classifications of the Carnivora by dividing the order into three suborders and five infraorders—the Procreodi, Acreodi, Pseudocreodi, and a new Amphicreodi (within the Creodonta); and an expanded concept of Eucreodi (including the suborder Fissipedia = Carnassidentia, and the suborder Pinnipedia). The Eucreodi were classified as an infraorder of the Fissipedia, although the text (Gregory and Hellman, 1939, p. 382) states that the Eucreodi could be expanded to include both Fissipedia and Pinnipedia, since "all the families of modern Carnivora were derived from one common ancestral stock" The suborders were referred to parenthetically in the Gregory and Hellman classification, and it is unclear whether this was for historical reference or for actual taxonomic utilization. Gregory and Hellman rejected the conservative horizontal system of classification used by Matthew, and they believed that their arrangement better reflected a phylogenetic approach to classification. The concept of the "Miacidae" was retained; however, it was placed in its entirety into the family Viverridae. The Greg-

ory and Hellman paper suggested the radical proposals of a subfamily Miacinae of the Viverridae, which included the genera previously contained in Matthew's Miacinae, whereas the Viverravinae were abandoned and *Viverravus* and *Didymictis* were placed within the subfamily Viverrinae (with the living civets). *Viverravus*, *Didymictis*, and *Ictidopappus* were believed to be very close relatives of the living Viverridae, and the Miacinae were considered to be more distant allies, but both groups were thought to be closer to the ancestry of the Feloidea Simpson (=Aeluroidea Flower) than to the Musteloidea Gregory and Hellman and Canoidea Simpson.

The most extensive, recent consideration of the Miacidae was in Simpson's (1945) classification of the mammals. This arrangement followed Matthew in recognizing the Miacinae and Viverravinae as subfamilies of the Miacidae. The family Miacidae was the only member of a superfamily Miacioidea (equivalent to Matthew's Eucreodi). Together with the superfamilies Canoidea (=Arctoidea plus Cynoidea of Flower, 1869) and Feloidea (=Aeluroidea of Flower, 1869) the Miacioidea formed a coordinate, tripartite division of the Fissipeda. Such an arrangement represented an important advance in the interpretation of the phylogeny of the Fissipeda. The classification of the Miacidae within this group explicitly recognized the closer relationship between the Miacidae and the more advanced Carnivora than between the Miacidae and Creodonta. An assumption of direct phyletic continuity between the Miacidae and other Fissipeda was proposed, and removal of the Miacidae from a position within the Creodonta allowed for the possibility that the Miacidae might not share a close phylogenetic history with the Creodonta.

Simpson's (1945) discussion of the Carnivora (including Creodonta, Fissipeda, and Pinnipedia) provided a selected history of the classificatory arrangements utilized until 1945, and a consideration of the philosophy he used in constructing the classification presented therein. Simpson dealt only briefly with most of the previous classifications, but

considered those of Matthew, and Gregory and Hellman in more detail. Most of Simpson's work on the Miacoidea, and much of his classification of the Creodonta was acknowledged as being based heavily on Matthew's numerous and extensive treatments of the Carnivora. Gregory and Hellman's (1939) arrangement of the Carnivora was considered the only radical departure from standard classifications, and was therefore thoroughly analyzed by Simpson.

The threefold division of the Carnivora, as used by Simpson and most previous workers, was replaced by a fivefold division by Gregory and Hellman (1939), as described above. Simpson accepted this as both logical and theoretically acceptable as a statement of carnivoran phylogeny. He believed, however, that the tripartite division was equally consistent and acceptable, more convenient, and more familiar. "Logic in classification is not solely concerned with making coordinate units of like antiquity or arising from the same dichotomy—indeed this ideal is impractical. There are other essential logical considerations, for instance, the desirability of approximate balance as to evolutionary status and distinctness This is a case where a compromise between horizontal and vertical classification is usual and seems to me advisable if not necessary" (Simpson, 1945, p. 218).

Simpson, like Matthew, stressed the importance of compromise in favor of horizontal classification. Arrangements which emphasized the vertical aspects of phylogeny and classification were lauded, but ultimately rejected.

Simpson's (1945) discussion of the Miacoidea points out the dichotomy between those that would classify the Miacidae horizontally with the Creodonta (including Cope, Schlosser, Matthew, and Simpson prior to 1945), and those that included the Miacidae vertically within the Fissipeda (Winge, Wortman, Scott, Osborn, and Simpson in 1945). Simpson here placed the Miacidae in the Fissipeda because he believed it was the arrangement "increasingly favored by my [Simpson's] colleagues" (p. 221), although he believed that this was only a formal taxo-

nomic change that did not alter the previous concepts of miacid phylogeny.

The only taxonomic study of the Miacidae that Simpson (1945) discussed in any detail was that of Gregory and Hellman (1939), primarily because it proposed the most significant change in the contemporary systematic usage. The suggestion that the Miacidae be included within the Viverridae was considered radical, and was rejected by Simpson. Simpson believed that only primitive characters allied the miacids with the Viverridae, and the group as a whole could be "structurally ancestral" (Simpson, 1945, p. 221) to the Feloidea and Canoidea.⁴

MacIntyre (1962) briefly discussed the morphology and systematics of the Miacidae, and named a new genus, *Simpsonictis*, based on material of *Didymictis tenuis* Simpson. His discussion pointed out that the Miacidae were generally considered the primitive stock for the modern Carnivora. The earliest miacids were members of the Viverravinae (although they were derived in the loss of M_3), but the Miacinae probably represented a closer approximation to the morphology of the ancestral miacid stock. The Viverravinae consisted of *Viverravus*, *Didymictis* and *Ictidopappus*. The description and discussion of the genus revealed that *Simpsonictis* could be considered a viverravine with various insectivorous dental specializations, but with similarities to smaller species of both *Viverravus* and *Didymictis*.

Later MacIntyre (1966) published a thorough and extensive review of the systematics of *Ictidopappus* and *Protictis* as the first part of an intended series on the evolution of the Miacidae. MacIntyre raised Matthew's subgenus *Protictis* to generic rank, and divided

⁴ Although the text reads "I prefer to express the relationships by placing the Miacidae in a separate superfamily from which both Feloidea and Viverroidea arose" (Simpson, 1945, p. 222), there is no such superfamilial taxon as Viverroidea in Simpson's classification (or any other author, as far as we are aware). We presume that since Simpson was discussing the relationship of the Miacidae to the Viverridae (Feloidea) and Canidae (Canoidea) in the preceding sentences, he mistakenly used the term "Viverroidea" instead of Canoidea.

this genus into three subgenera—*Protictis* (*Protictis*), *P.* (*Simpsonictis*), and *P.* (*Bryanictis*). The designation of *Simpsonictis* as a subgeneric member of *Protictis*, and the erection of a new subgenus *P.* (*Bryanictis*) to include "*Didymictis*" *microlestes* and a new species *P.* (*Bryanictis*) *vanvaleni*, greatly broadened the concept of the taxon *Protictis* and restricted the scope of *Didymictis*.

MacIntyre (1966) considered the relationship of the Miacidae to the Creodonta and Fissipeda, and favored the vertical classification of the family with the Fissipeda, as advocated by Simpson (1945). Even though he stated that he believed a vertical classification best portrayed the phyletic relationships of the Miacidae, he did not attempt to analyze or organize the members of the paraphyletic Miacidae using a vertical or phylogenetic methodology.

MacIntyre (1966, pp. 195–205) in his general discussion listed characters that could be hypothesized as primitive in the common ancestor of the Miacinae and Viverravinae. Many of these are probably primitive for eutherians, in general, although with further analysis some of the dental and cranial features might be determined to be derived for the Miacidae (and possibly other Carnivora, as well). Following that section, MacIntyre considered the actual possibilities for miacid ancestry in the known Cretaceous taxa (p. 203). The problem of the interpretation of P_4 morphology was thoroughly and accurately discussed, but no definitive conclusion was drawn as to whether a simple or a "molari-form" P_4 was primitive for the Carnivora. A simple P_4 had been assumed primitive for therians by most workers, and MacIntyre provisionally accepted this convention for the ancestral carnivoran. Under that scheme *Cimolestes* appeared to exhibit the closest approximation to the expected ancestral morphology for all later Carnivora.

A number of other shorter papers have been written which considered the relationships of various genera of supposed members of the Viverravinae.

Teilhard de Chardin (1915) recognized "*Viverra*" *angustidens* from France as a

member of the Viverravinae and placed the species in the genus *Viverravus*. In 1945 Kretzoi erected a new genus, *Quercygale*, for "*Viverravus*" *angustidens*. Apparently unaware of the paper by Kretzoi, de Beaumont (1965) designated "*V.*" *angustidens* as the type species of a new genus, *Humbertia*, and named another species, *H. helvetica*. The next year de Beaumont (1966) realized that *Humbertia* was synonymous with Kretzoi's *Quercygale*. Nevertheless, de Beaumont's 1965 paper included an excellent comparative chart of the many differences distinguishing "*Humbertia*" from "*Viverravus*"; proposed the hypothesis that "*Humbertia*" was derived from North American *Didymictis*, rather than *Viverravus*; and recognized that "*Humbertia*" was very similar morphologically to *Tapocyon*.

Van Valen (1967) included a brief reference to the relationship of *Quercygale* in his broader paper on the classification of the insectivorans. Van Valen felt that *Quercygale* should be considered a subgenus of, or member of the genus, *Tapocyon*. The lack of an M_3 in a miacine (*Quercygale*) led Van Valen to conclude that the Viverravinae could not be unambiguously distinguished from the Miacinae (which he presumably differentiated only on the presence or absence of M_3). Van Valen also considered Kretzoi's (1945) *Quercygalidae* a synonym of the Miacinae.

In his discussion of the origins of placental carnivores, Van Valen (1969) compared the morphology of various "miacids" with the Cretaceous genera *Protungulatum*, *Cimolestes*, and *Procerberus*. He also erected a new tribe Ictidopappini within the Miacidae to include *Ictidopappus*, and resurrected *Simpsonictis* as a valid genus distinguishable from *Protictis*.

An analysis of the fauna from the Upper Eocene Headon Beds of England by Cray (1973) included a discussion of *Quercygale* and the addition of "*Viverra*" *hastingsae* Davies as a species of *Quercygale*. Cray disregarded Van Valen's suggestion that *Quercygale* be considered a subgenus of the miacine *Tapocyon* by retaining *Quercygale* as a distinct genus within the Viverravinae.

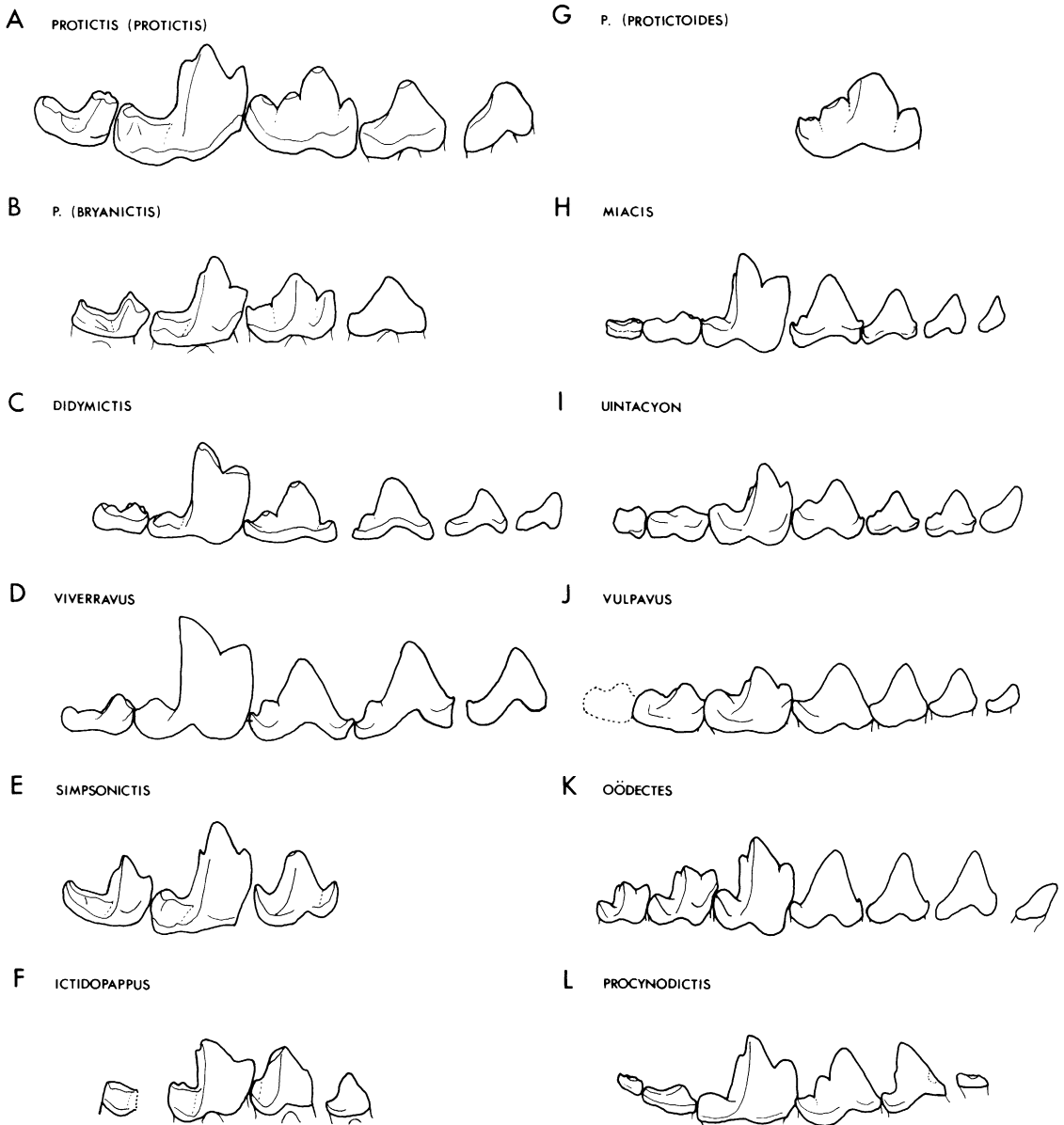


FIG. 2. Comparison of lower dentitions of early Tertiary Carnivora. The first molar of each series is drawn to approximately the same size, and the dentitions are aligned vertically along the anterior edge of the first molar. The species and specimen numbers used as representatives for the genera are: A) *P. (P.) haydenianus*, AMNH 3371, 16540; B) *P. (B.) microlestes*, AMNH 11521, USNM 9302; C) *D. protenus*, AMNH 2831; D) *V. sicarius*, AMNH 11521; E) *S. tenuis*, AMNH 35349 and 35350, USNM 9097; F) *I. mustelinus*, USNM 9296; G) *P. (P.) aprophatos*, AMNH 105371; H) *M. parvivorus*, AMNH 11496; I) *U. vorax*, AMNH 11507, 12620; J) *V. profectus*, AMNH 12626; K) *O. herpestoides*, AMNH 11495; L) *P. vulpiceps*, AMNH 2514. This figure is partially adapted from Matthew, 1909, p. 347. Buccal view of right dentitions; anterior toward right of page. Specimens A, B, E (in part) and L have been reversed during drawing.

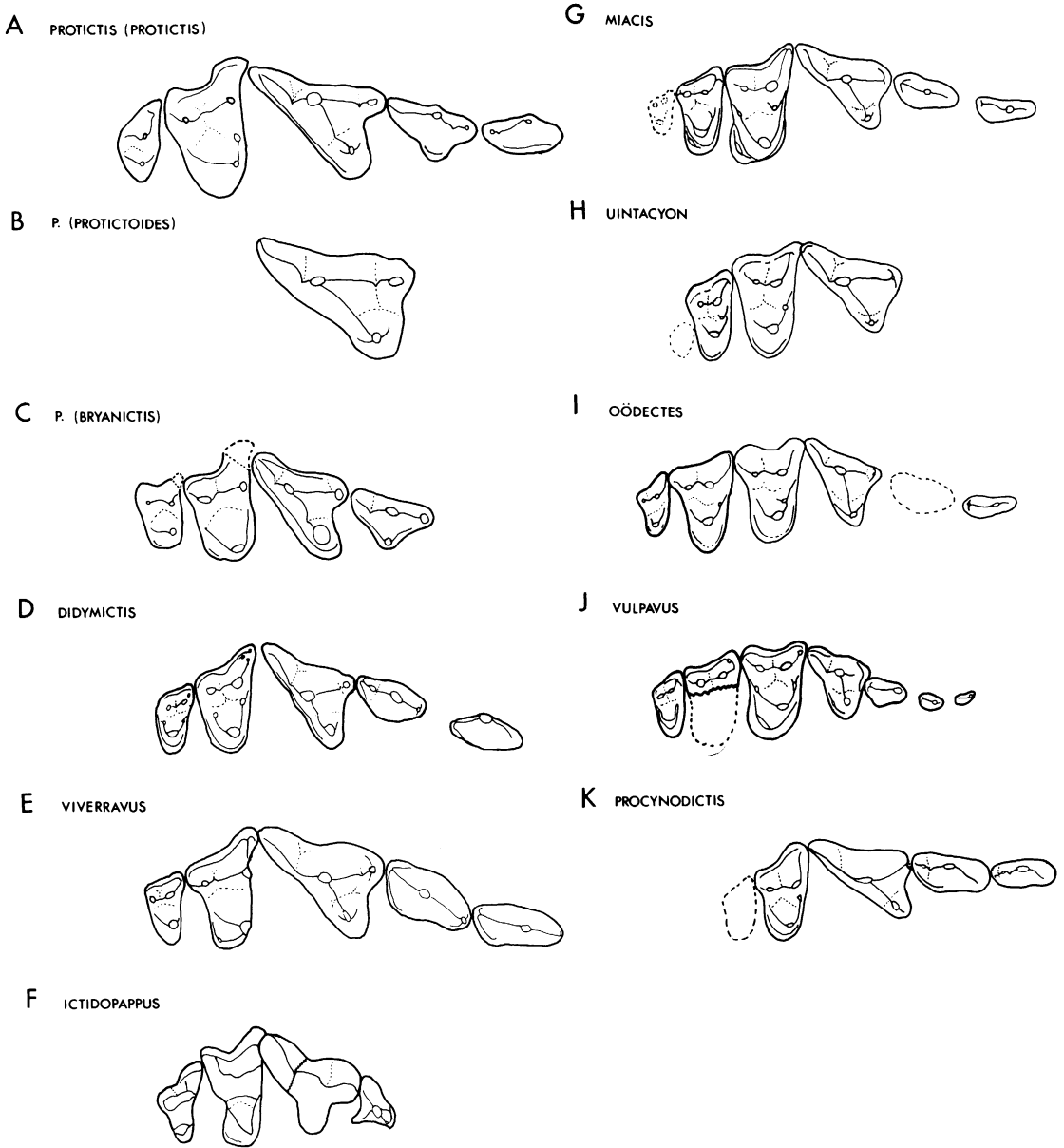


FIG. 3. Comparison of upper dentitions of early Tertiary Carnivora. The first molar of each series is drawn to approximately the same size, and the dentitions are aligned vertically along the anterior edge of the first molar. The species and specimen numbers used as representatives for the genera are: A) *P. (P.) haydenianus*, AMNH 3368, 16540; B) *P. (P.) aprophatos*, AMNH 97701; C) *P. (B.) microlestes*, AMNH 35361, 35362; D) *D. protenus*, AMNH 2831; E) *V. sicarius*, AMNH 11521; F) *I. mustelinus*, USNM 9295; G) *M. parvivorus*, AMNH 11500; H) *U. vorax*, AMNH 11507, 12620; I) *O. herpestoides*, AMNH 11495; J) *V. profectus*, AMNH 12626; K) *P. vulpiceps*, AMNH 2514. This figure is partially adapted from Matthew, 1909, p. 344. Crown view of right dentitions; anterior toward right, buccal toward top of page. Specimens A, C, F, and K have been reversed during drawing.

PREVIOUS DEFINITIONS OF THE MIACIDAE

The previous classifications of the Miacidae are thoroughly discussed in the Historical Review section of this paper. However, consideration of the characters used by various workers to define the Miacidae and its subdivisions is interesting and useful to the present categorization of the various "miacid" taxa. Those authors did not distinguish between derived and primitive features in their taxonomic definitions. The original definitions and characterizations of relevant taxa are presented in this section, whereas features uniquely derived and diagnostic for various carnivoran taxa are discussed in more detail later in this paper. Figures 2 and 3 provide comparative drawings of the dentitions of representative genera of early Tertiary Carnivora. Many of the features discussed here and in the systematics section below are also illustrated.

In Cope's (1883) discussion of the Creodonta he defined the Miacidae as creodonts with tubercular upper molars, sectorial last upper premolar, and a tubercular sectorial first lower molar. He subdivided the Miacidae into the genera *Miacis* and *Didymictis* and characterized them as having, respectively, two inferior tubercular molars and four premolars, and one inferior tubercular molar and four premolars. The discussion of *Miacis* included this description: lower dentition consisting of I_3 C_1 PM_4 M_3 ; single-rooted first premolar; M_1 with a broad heel, one edge submedian and a little elevated above the other; and M_{2-3} tubercular with conic tubercles anteriorly and a short heel. The description of *Didymictis* included: "Inferior molars six, consisting of four premolars and two true molars. True molars, a posterior tubercular, and an anterior tubercular-sectorial, i.e., with three elevated cusps and a posterior heel. Premolars with a lobe behind the principal cusp. The canine teeth are directed forwards, and are very close together, so that it is doubtful whether there were any incisors. An ungual phalange of the typical species is strongly com-

pressed" (Cope, 1883, pp. 304–305; 1875a, p. 11; and 1877, p. 123).

Wortman and Matthew's (1899) proposal of a new family Viverravidae stressed the similarity of the members of this family to the Viverridae in the basicrania, dental formula and pattern, atlas and vertebral artery, and limb structure. They considered distinctive the deep vertical notch in the metastyle blade of P^4 and the presence of a large P^4 parastyle, in both families. The Viverravidae were distinguished from the creodonts by the presence of P^4/M_1 sectorial, from "early Canidae" (=Miacinae of Matthew, 1909) by the parastyle on P^4 and presence of only two molars, and from the Viverridae by the retention of the primitive free scaphoid, lunar and centrale.

Wortman (1901) included the Viverravidae and Fissipedia (including the "miacines") in the carnivoran suborder Carnassidentia. His definition of the suborder was carnassial teeth present and always consisting of P^4/M_1 ; scaphoid, lunar, and centrale generally united; ungual phalanges compressed and pointed. The Viverravidae were characterized by the lack of a hypocone and a molar formula of either 3/3 or 2/2 (since *Oödetes*, with three molars, was considered a viverravid), in addition to the characters cited above from Wortman and Matthew (1899). The Viverravidae were distinguished from the contemporary "Canidae" by the perforation of the transverse process of the atlas for the passage of a vertebral artery and a well-developed P^4 parastyle, both of which were considered "entirely distinctive" (p. 143) characters. Furthermore, the lack of curvature in the femur, and the total absence of a hypocone on the upper molar differentiated the viverravids from the canids.

Matthew (1901a) considered the Palaeonictidae, Arctocyoniidae, and Viverravidae as members of the Creodonta Adaptiva defined by P^4/M_1 carnassial, when present; claws of modern type and carried free of the ground; and scapholunar-centrale early becoming united. In the Viverravidae the post-carnassial teeth were assumed to be "becoming tubercular" (Matthew, 1901a, p. 59).

The extensive monograph by Matthew (1909) provided a good deal of information on miacid taxonomy. Matthew included the Miacidae and Arctocyoniidae in the Eucrodi of the Creodonta. The Miacidae possessed the following creodont characters: scaphoid, lunar and centrale generally distinct; third trochanter on the femur; entepicondylar foramen on the humerus; small brain; unossified tympanic bulla; and toes 5-5. The diagnostic characters of the family Miacidae included P^4/M_1 carnassials as in modern Carnivora; postcarnassial teeth generally tubercular; metacone smaller than protocone; ungual phalanges compressed and unfissured at the tips; and paraxonic digit symmetry. Within the Miacidae, the members of the subfamily Viverravinae were distinguished by the molars reduced to 2/2; large antero-external cusp (parastyle) on P^4 and posterior accessory cusp on P_4 ; elongate skull; presence of a calcaneal fibular facet; and other features of the limb morphology. In contrast, the Miacinae had a full molar complement of 3/3; the antero-external cusp of P^4 either rudimentary or absent; skull length moderate or short; absence of a calcaneal fibular facet; and other differences in limb structure. The Miacinae were further divided into Cercleptoidei and Cynoidei; the first had the carnassial only weakly differentiated, and the molars were all of similar form, whereas the second group had well-differentiated molars and tubercular posterior molars. Matthew regarded the split of the Miacidae into the Miacinae and Viverravinae as the beginning of the differentiation into the arctoid and aeluroid Carnivora, respectively. The Cynoidei were further believed to be the precursors of the Cynoidea, whereas the Cercleptoidei were considered ancestral to the Arctoidea proper.

Matthew's (1915) paper included keys to the families of Creodonta, genera of Miacidae, and species of *Didymictis*. The key for the Creodonta included the divisions Procreodi, Eucrodi, Pseudocreodi, and Acreodi, distinguished by differences in the ungual phalanges, and further characterized by features of the carnassials. The Miacidae were

the only family placed in the Eucrodi, were distinguished by the lack of fissuring in the ungual phalanges, and were characterized by the carnassials being P^4 and M^1 (*sic*—we assume he is referring to M_1 , and that this is just a printer's error in the publication). Within the Miacidae the genera were split into two major groups corresponding to the Viverravinae and Miacinae, although the two groups were not explicitly named in the key. One group (Viverravinae) included *Didymictis* and *Viverravus* and was distinguished by the prominent antero-external cusp of P^4 , the elongate oval shape of M_1 , and the presence of two upper and lower molars. The other group (Miacinae) contained *Uintacyon*, *Miacis*, *Vassacyon*, *Oödetes*, *Vulpavus*, and *Palaeoarctonyx* and was distinguished by the absence or weak development of the antero-external cusp of P^4 , the short-oval or round shape of M_2 and M_3 , and the presence of three upper and lower molars.

Simpson's (1945) new superfamily Miacoidae did not include any formal diagnosis or description of the taxon, except a statement that it was proposed to include the Miacidae, the primitive precursors of the later Carnivora.

All the workers cited above have presented morphological characters that may ally the Miacidae with the more advanced fissiped Carnivora. Furthermore, they all dichotomously divided the Miacidae into two major groups. Each of these groups was believed to be ancestral to one of the two major branches of living carnivorans by some workers. However, all the above studies retained all the early Tertiary Carnivora within a single, horizontally arranged family. The members of this family Miacidae were either classified with, and considered ancestral to, the Fissipeda, or placed within the Creodonta because of their overall morphological similarity to and supposed recency of common ancestry with other Creodonta. We believe that the family Miacidae is a paraphyletic grouping of generally morphologically primitive but not closely related taxa. The taxa previously included within the Miacidae have clear phyletic relationships with the lat-

er, more advanced Carnivora. Therefore, we propose abandonment of the use of the family Miacidae to include all primitive, early Tertiary Carnivora. Furthermore, the use of the Miacidae, or the term miacid, as a wastebasket taxon in future taxonomic, phylogenetic, and evolutionary studies is discouraged. The retention of a non-monophyletic taxon should be avoided, and we propose a hypothesis of relationship for all the taxa previously included within the Miacidae. Concise, explicit, and testable definitions of taxa and hypotheses of relationships are essential to the understanding of the evolutionary history of the Carnivora.

SYSTEMATICS

ORDER CARNIVORA BOWDICH, 1821

INCLUDED TAXA: Feliformia and Caniformia.

DISTRIBUTION: ?Early Paleocene to Recent.

DIAGNOSIS: Eutherian mammals differing from all other mammals in the following derived characters— P^4/M , modified as the principal carnassial teeth, lacking a migratory locus for the carnassial as found in the Creodonta, but with retention of some subsidiary shear on other teeth; P^4 protocone located anterolingually, far forward of the paracone; extremely elongate P^4 metastyle wing with a well-developed metastyle blade and carnassial notch; well-developed, elongate P_4 talonid with at least two posterior accessory cusps; M_{2-3}^{2-3} reduced in size; processus hyoideus formed by a ventromedial prolongation of the squamosal.

Primitive features for the Carnivora: retention of M_{1-3}^{1-3} ; P^4 with a small, but distinct parastyle cusp; P^3 lacking a protocone; all molar talonids short, basined, with a large hypoconid as the highest talonid cusp, and an obliquely oriented cristid obliqua; molar trigonids high, with the paraconid < metaconid < protoconid size; molar paraconids and metaconids moderately closely appressed, resulting in a closed-V between the paralophid and protolophid in the trigonid; upper molars with both a paraconule and metaconule; molar hypocones absent as dis-

tinct cusps, precingulum and postcingulum not continuous around lingual base of protocone; small P_4 anterior accessory cusp; P_4 lingual accessory cusp absent; entotympanic bulla unossified; scaphoid, lunar, centrale separate; calcaneal fibular facet present; scapula without teres major process or secondary scapular spine.

DISCUSSION: Although Flower (1869) limited the concept of the group Carnivora to the living Aeluroidea, Arctoidea, and Cynoidea, the earliest workers to consider the relationships of fossil taxa included the Creodonta as a suborder of the Carnivora (for instance, Cope, 1880a; Trouessart, 1885). Van Valen (1966) and Tedford (1976) have recently excluded the Creodonta from the Carnivora; we agree with this exclusion and restrict the concept of Carnivora to those taxa previously included within the Miacidae, Fissipeda, and Pinnipedia. The construction and definition of a monophyletic taxon, Carnivora, that includes both the living and fossil "miacids," "pinnipeds," and "fissipeds," but excludes the Creodonta and all other mammals, is very difficult. It is essential, however, to construct monophyletic groups that are explicitly and rigorously diagnosed and are readily subject to critical review by other workers. Tedford's (1976) consideration of the relationships of the carnivorans was an important first attempt at such an arrangement. However, his diagnoses of the order Carnivora, and suborders Feliformia and Caniformia excluded the members of the Miacidae from a phyletic position within these groups, as all of the known miacids appear to lack an ossified entotympanic. In the above diagnosis, we characterize the order Carnivora in such a way that the taxon remains a monophyletic assemblage that includes the Miacidae, but excludes the Creodonta. For a graphic representation of the phylogeny hypothesized for all Carnivora, see figure 4.

The phylogeny and taxonomic diagnoses presented in this paper were determined by a cladistic analysis of the entire Carnivora, and for lower level taxa within the Carnivora. The primitive to derived polarity of the characters used in this analysis was ini-

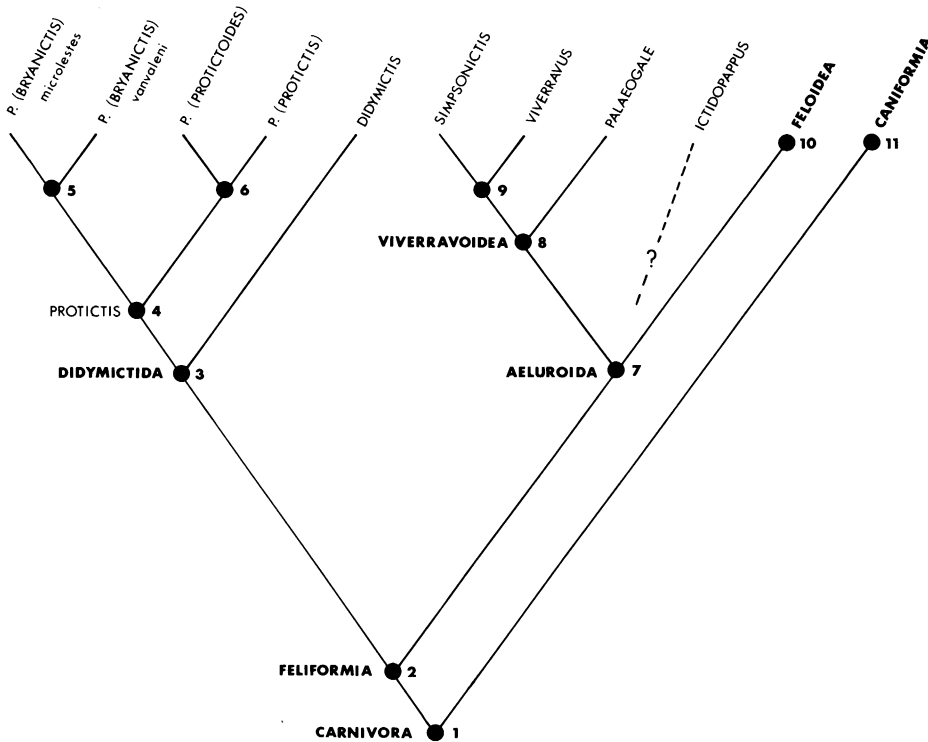


FIG. 4. Proposed phylogenetic relationships of the Carnivora. The numbers at the nodes refer to taxa and character distributions summarized in the Phylogeny section of this paper (see Systematics section for detailed discussions). Genera and species are in lightface type and higher level taxa are in boldface type.

tially determined through comparison to the character distributions in a number of possible outgroup taxa (including Creodonta, Metatheria, *Cimolestes*, *Didelphodus*, *Procerberus*, *Gypsonictops*, *Protungulatum*, *Avunculus*, *Purgatorius*, *Leptonysson*, *Didymoconus*, and others).

Following the generation of an initial hypothesis of phylogeny based on these character distributions, we analyzed the congruence of polarity determinations and distribution of characters, with the phylogeny. Some of the initial polarity assignments resulted in character distributions that were incongruent with the phyletic arrangement of taxa supported by the distribution of the majority of the other characters. The most parsimonious arrangement of character distributions among taxa was accepted as the least

contradicted hypothesis of phylogeny. In cases in which polarity assignments resulted in character distributions that were extremely incongruent, we considered the original hypotheses of polarity refuted rather than accepting numerous independent acquisitions or losses for these features.

Occasionally, two character states found within the Carnivora will also be found in outgroup taxa; in such cases, the conflict is resolved by restricting the outgroup (generally to *Cimolestes* and the Creodonta under the testable assumption that these taxa may be more closely related to the Carnivora than are the other outgroup taxa) or by internal parsimony (minimizing the number of character conflicts between taxa within the Carnivora). These conflicts emphasize the need for more intensive analysis of possible char-

acter reversal or nonhomology (convergence) in these features. Our final hypotheses of character polarity, character distribution and phylogeny are presented below, and any contradictions of the *a priori* polarity assignment based on outgroup comparisons are noted in the text.

Watrous and Wheeler (1981) provide a good formalization of a similar method of determining character polarity and analyzing character distributions in a cladistic analysis. We particularly agree with their (1981, p. 9) belief that cladistic analysis is generally a step-by-step process in which many character polarity and distribution determinations are dependent on preceding polarity decisions and taxonomic clustering (clustering based on other character distributions—their “Functional In-Group (FIG)/Functional Out-Group (FOG)” concept).

The development of P^4 and M_1 into the principal shearing pair, or carnassials, is highly modified from the condition found in creodonts and various “insectivores.” In other sectorial mammals, shear may be developed on all molars and some premolars, or isolated on a single carnassial pair. In various true insectivores and Cretaceous eutherians, shear is distributed throughout the cheek tooth row, without the isolation of a single carnassial pair of teeth (in particular, P^4/M_1). The Hyainodontidae and Oxyaenidae in the Creodonta develop principal carnassial pairs of M_3^2 and M_2^1 , respectively, although subsidiary shear is retained on the more anterior teeth. Furthermore, in the Creodonta, these teeth represent only the terminal pair of carnassials, in a sequence in which the primary shear locus moves posteriorly during ontogeny (Mellett, 1977). In the Carnivora, the sole carnassial pair is uniquely developed as P^4/M_1 and shear is maintained at this locus only, throughout life.

The protocone on P^4 of carnivorans is located far anterolingually on the tooth crown, far forward of the apex of the paracone, and frequently medial or anterolingual to the parastyle. In *Didymoconus* and *Kennalestes* the protocone of P^4 is located posterolingual to the paracone apex, whereas in *Gypso-*

nictops (AMNH 105158), *Didelphodus* (AMNH 4228), *Cimolestes* (AMNH 101992, 105156, 105152), and the Creodonta (e.g., *Proviverra*, AMNH 13142) the protocone is directly medial, or slightly anterolingual to the paracone. The extreme anterior position of the protocone of P^4 is derived, and is characteristic of primitive Carnivora.

The extreme elongation of the metastyle wing on P^4 and concurrent development of an elongate shearing blade and distinct carnassial notch is derived for the Carnivora. This distinctive metastyle morphology is found in the molars of the Creodonta in connection with the carnassial function of those teeth. The metastyle of P^4 in the Creodonta is also modified, but to a lesser degree, by slight elongation into a shearing blade and development of a shallow carnassial notch. This character may ally the Creodonta to the Carnivora, as no other mammals elaborate the metastylar region of P^4 in the same manner, or to the same extent. *Cimolestes* and *Didelphodus* elongate the metastyle to a slight to moderate degree, but do not develop a distinct blade and notch. The Carnivora develop a metastyle blade that is more elongate and a notch that is deeper than that found in any of the Creodonta or the Cretaceous eutherians.

An elongate, well-developed talonid on P_4 is here considered a derived character uniting all Carnivora, and therefore is primitive for the taxa included within the order. The talonid is relatively broad, rimmed posteriorly and lingually by a strong cingulum, and there are two posterior accessory cusps present along the labial ridge running from the posterior margin of the main cusp. The presence of these two posterior accessory cusps results in the formation of two distinct notches, between the main cusp and the first posterior accessory cusp, and between the first and second posterior accessory cusps (see fig. 1 for premolar terminology). A small cusp or cusplule may have been developed from the posterior cingulum in the earliest Carnivora, but the patchy distribution of this character throughout the Carnivora makes it unclear whether this is a derived feature for the entire Carnivora, or whether it is evolved

independently as an advanced character within some carnivoran taxa.

A simple P_4 has been hypothesized as primitive for carnivorans (see discussion in MacIntyre, 1966, p. 204), particularly in regard to the trigonid of P_4 . Outgroup comparison did produce an *a priori* hypothesis that a simple P_4 is primitive. An elaborate P_4 talonid is not found in any of the outgroups *Cimolestes*, *Didelphodus*, *Leptonysson*, or the Creodonta; the talonids are very short, narrow, and generally have only a single, posteriormost cingulum cusp. The arrangement of the cusps on the talonid of P_4 in carnivorans lacks the structure normally developed in the molar talonids, as they are aligned in a straight, or slightly arcuate, anteroposterior line and are without a simple analogy to the molar cusps. In the earliest Carnivora P_4 was elaborated, particularly in the talonid, but it was not a molariform tooth.

However, the results of this study indicate that an elaborate P_4 talonid may be the primitive state for Carnivora. The elaborate talonid structure described above is found widely in the early Tertiary carnivorans previously assigned to the "Miacidae" in both the "Viverravinae" (members now assigned to the Feliformia, see below) and the "Miacinae" (members assigned to the Caniformia, see below), although various members of both suborders may later simplify and reduce P_4 . *Protictis* (*Protictis*) *haydenianus*, *P. (Bryanictis)* *microlestes*, *Miacis* *hargerii*, *Procyonictis* *vulpiceps*, *Uintacyon* *massetericus*, and a new subgenus of *Protictis* from the Eocene of northwest Wyoming all have an elaborate P_4 talonid with two posterior accessory cusps. Many other "miacids" also have a well-developed, elongate P_4 talonid, although the second posterior accessory cusp is not present in these forms.

All Carnivora have greatly reduced the size of M_{2-3}^2 relative to the size of P_4 and M_1^1 . The trigonid height on M_{2-3} versus M_1 is also reduced relative to the primitive eutherian condition, as is the ratio of M_{2-3} trigonid height/tooth height. Primitively M_{1-3}^1 are approximately equal in size, or $M_1^1 < M_2^2 < M_3^3$ size. In *Kennalestes* and *Gyp-*

sonictops M_{1-3} are approximately equal in size, although M_1 is slightly smaller than M_2 in both genera, and the trigonids are high on all the molars. *Procerberus* and *Cimolestes* have M_1 approximately equal in size to M_3 , both of which are slightly smaller than M_2 in *Procerberus* and slightly larger than M_2 in *Cimolestes*. In *Protungulatum* and *Purgatorius* the M_1 and M_2 are about equal in size, and in both genera these teeth are smaller than M_3 . Members of the Paenungulata also primitively have $M_1 < M_2 < M_3$ size. The extreme reduction of M_{2-3}^2 size (relative to M_1^1) in Carnivora is obviously derived over the primitive condition exhibited by the taxa mentioned above.

All the Carnivora may be united by the development of a processus hyoideus as a process of the squamosal, which extends ventromedially to contact the promontorium. This squamosal process forms the anterior margin of the stylomastoid foramen, and the facial nerve exits the auditory region posterior to the process. A squamosal processus hyoideus is found in the primitive carnivorans *Viverravus*, *Vulpavus*, and *Didymictis* and in more derived Carnivora, whereas in most other mammals the processus hyoideus is formed, instead, from the mastoid portion of the petrosal. Work in progress by R. L. Cifelli indicates that development of this squamosal process may be uniquely derived for the Carnivora. The elaboration of a processus hyoideus in mammals may range from a process that completely bridges over the facial canal to contact the promontorium, to a simple swelling of the petrosal external to the facial canal. The tympanohyal, the most cranial element of the hyoid apparatus, is either fused to, or articulates with the processus hyoideus.⁵

⁵ The developmental relationship between the tympanohyal and the processus hyoideus is complex, and the distribution of modes of development of the two is highly variable within the Mammalia (see van der Klaauw, 1931). Because of this workers have variably called a bony swelling or process in this area a processus hyoideus, a tympanohyal, a tympanohyal process, etc. We prefer the use of processus hyoideus as a descriptive morphologic term, without inherent developmental implications.

Ursids differ from other Carnivora in the development of a processus hyoideus posterior to the exit of the facial nerve. The process in ursids thus forms the posterior margin of the stylomastoid foramen.

Comparison of the morphology of the taxa united by the derived features discussed above, with that of outgroup taxa permits a hypothesis of primitive character states that are retained in the Carnivora. The full eutherian molar complement $M_1^1\text{--}M_3^3$ is retained in early carnivorans; although the members of the feliform branch lose M_3^3 , many caniforms retain M_3^3 throughout their phyletic history.

Some members of both the feliform and caniform lineages retain a small, distinct, anterolabial basal parastyle cusp on P^4 . A small parastyle is present on P^4 in all the outgroups examined, and this morphology may be hypothesized as primitive for Carnivora. Later carnivorans modify the parastyle in at least two different and distinctive manners. The large protocone found on P^4 of all the outgroups would also be primitive for all carnivoran taxa.

P^3 would lack a distinct protocone cusp, but would have a well-developed posterolingual cingulum at the base of a slope and shelf that extends lingually from the posterior base of the paracone. *Gypsonictops* and *Didelphodus* have a protocone cusp on P^3 , in *Cimolestes* the protocone of P^3 is variably present in different species, but the protocone is absent in the Creodonta. In *Proviverra* and *Sinopa* P^3 is very similar to the morphology proposed for the early Carnivora and found in most "miacines"; a protocone is absent, and a large cingulum is developed on the posterolingual margin of the tooth. In known primitive Carnivora a protocone on P^3 is found only in *Protictis*, while all other genera lack this cusp. Therefore, the polarity for the presence or absence of the protocone on P^3 for the Carnivora is uncertain. However, the limited distribution of this character within the Carnivora and the absence of the protocone in the Creodonta and some *Cimolestes* would support the hypothesis that the absence of the protocone is a primitive retention for carnivorans. Any subsequent

elaboration of the posterolingual cingulum, or development of an antero- or medio-lingual protocone would be derived within the Carnivora.

In all the outgroups investigated the molar trigonids are high, the paraconid size < metaconid size < protoconid size, the paraconids and metaconids are fairly closely appressed, and the angle between the paralophid and protolophid forms a closed-V in the trigonid. The trigonid on M_2 , however, is much lower than the trigonid on M_1 , and this may represent a character derived for the Carnivora, with respect to the primitive condition in the outgroups in which all the trigonids are subequal in height. The molar talonids are always shorter in length than the trigonids, the hypoconids are robust and are the largest talonid cusps, the talonids are well basined lingually, and the cristid obliqua are aligned oblique to the anteroposterior axis of the tooth. This morphology is also widespread in both primitive Feliformia and Caniformia, and may be considered the primitive molar morphotype for the Carnivora.

The upper molars of most carnivorans retain the metaconule and paraconule found widely in eutherian molars. Molar hypocones are not developed as distinct cusps on the posterolingual margins of the protocone. However, a well-developed postcingulum and precingulum were probably present in the earliest Carnivora, but the two cingulae were not continuous around the base of the protocone. This hypothesized upper molar morphology would be similar to that found in early eutherians that have not yet strongly modified the molars from the primitive tribuccular mammalian pattern.

The carnivoran P_4 probably retained the primitive condition of a small anterior accessory cusp ("paraconid") and lack of a lingual accessory cusp ("metaconid") found in most early eutherian mammals. *Cimolestes*, *Didymoconus*, *Purgatorius*, *Avunculus*, and Creodonta lack a lingual accessory cusp on P_4 ; *Didelphodus* has this cusp variably developed; whereas *Protungulatum* has a large lingual cusp on a molariform trigonid. When it is present, all the groups have a small, low anterior accessory cusp, or only an anterior,

basal cingulum as in many creodonts. Within the Carnivora, most species have a very small, basal anterior accessory cusp, while only *Protictis* (*Bryanictis*) *vanvaleni* has a distinct lingual accessory cusp. We agree with MacIntyre's (1966, p. 204, and above) conclusion that a simple P_4 trigonid is a primitive eutherian condition retained in carnivorans, but the carnivoran talonid is primitively elaborated in a unique way. Comparison with outgroups reveals a conflicting character polarity, dependent on the particular taxon that is chosen as an outgroup. We recognize this conflict, but think that the presence of a simple P_4 in *Cimolestes*, *Didymoconus*, *Purgatorius*, *Avunculus* and the possible close relatives of the Carnivora, the Creodonta, and the derived state of the very molariform premolars in *Protungulatum*, provide strong evidence that a simple P_4 trigonid may be primitively retained in the Carnivora.

An unossified entotympanic bulla is presumed a primitive retention in the Carnivora. The little available evidence from Cretaceous eutherians indicates that an unossified bulla was widespread in early mammals. Furthermore, the absence of an ossified bulla in known skulls of early Caniformia and Feliformia ("miacids") such as *Vulpavus* and *Viverravus* indicates that the common ancestral stock of these two lineages would also have lacked an ossified entotympanic bulla. However, the present sample of well-preserved basicrania in early carnivorans is very small and the absence of intact ossified bullae may be an artifact of preservational and sampling biases. It is possible that larger samples of extremely well-preserved material of early carnivorans will reveal an ossified bulla, as has happened in the past with other groups (e.g., leptictids, see Novacek, 1977). Large collections of the basicrania of the Nimravidae indicate only partial ossification of the bullae,⁶ which would also reinforce the possibility that an unossified, or only partially ossified, entotympanic bulla

would be primitive for the Carnivora. Therefore, based on present evidence of the distribution of ossification in the ear regions within the Carnivora, and in the available Cretaceous outgroups, it appears that an unossified bulla would be characteristic of the earliest carnivorans.

In the feet, the Carnivora primitively retain an articular facet on the calcaneum for the fibula, and separate ossification of the scaphoid, lunar, and centrale bones. Both of these conditions are found in primitive eutherians and metatherians, as well as early carnivorans. Marsupials have a well-developed articulation between the calcaneum and a lateral process of the fibula, as do *Provillea* (and other Creodonta), *Protungulatum* (Szalay and Decker, 1974), *Asioryctes* (Kielan-Jaworowska, 1977), and the primitive feliform *Didymictis*. Both Novacek (1980) and Szalay and Decker (1974) consider the presence of a large calcaneal fibular facet to be primitive for the Theria: "The articulation of the fibula with the tarsus in *Protungulatum* is with both the astragalus and calcaneum, and this is undoubtedly primitive for the Eutheria and other Mammalia" (Szalay and Decker, 1974, p. 237). The calcaneal fibular facet is well developed in primitive feliforms, and in some living Feloidea, as well. *Didymictis* retains the primitive morphology for this feature; there is a well-developed, wide articular surface on the calcaneum, and a large facet on the laterodistal end of the fibula for articulation with the calcaneum. This is very similar to the condition in marsupials and creodonts, although the distal end of the fibula is simpler and more reduced in the Feliformia. *Paguma*, *Herpestes*, and *Viverra* also retain this calcaneal fibular articulation, although it is not as strongly developed in these forms as in *Didymictis*, and the surface area of the facet on the calcaneum is much smaller. The degree of ossification of the scaphoid, lunar and centrale has served as an important character in the early classifications of the Carnivora (including the Creodonta, see Historical Section). It is obvious, however, that the separate ossification of these bones is a primitive condition found in metatherians, all early eutherians, Creodon-

⁶ Hunt (1974a), however, believes that this is only an artifact of preservation, and that the Nimravidae would have had a totally ossified bulla in life (see below).

ta, and early feliform and caniform Carnivora. Fusion of the scaphoid and lunar into a single scapho-lunar bone probably occurred independently in both lineages of Carnivora, but may possibly be used to unite taxa within these lines.

The primitive carnivoran scapula would have a large primary scapular spine separating the infraspinous and supraspinous fossae, possess a straight axillary border, and lack a teres major process and any indication of a secondary scapular spine (see Caniformia section for further discussion of scapular morphology). This primitive scapular morphology is found in many members of mammalian outgroup taxa such as the Creodonta, Metatheria, Rodentia, Perissodactyla, Artiodactyla, and "condylarths."

The previous discussion of characters in the earliest Carnivora is critical to an understanding of the distribution of morphologies and the phyletic history of the included carnivoran taxa. Once the general morphotype for the Carnivora has been hypothesized, including both primitive characters retained from earlier evolutionary stages and characters uniquely derived for members of the Carnivora, all of these characters may be assumed to be primitive for taxa within the order Carnivora. The distribution of derived characters is analyzed below in order to determine the distribution of monophyletic taxa included within the Carnivora. The remainder of this systematic section is based on such an analysis, as is the construction of the hypothesis of relationship presented later in this paper.

SUBORDER FELIFORMIA KRETZOI, 1945

INCLUDED TAXA: Infraorders Didymictida and Aeluroida.

DISTRIBUTION: ?Early Paleocene to Recent.

DIAGNOSIS: Carnivorans differing from all other Carnivora in the development of the following derived features— P^4 parastyle enlarged; very deep, narrow, slitlike carnassial notch in the metastyle blade of P^4 ; M_3^3 lost in all taxa; M^2 reduced in size, and more simple in morphology; M_2 talonid extremely

elongate, entire tooth with elongate oval outline; M_2 hypoconulid larger than, or equal to, hypoconid size (particularly height).

Members of the Feliformia primitively retain these carnivoran characters: lack of molar hypocones as distinct cusps, precingulum and postcingulum not continuous around lingual base of protocone; P^4 protocone large; calcaneal fibular facet well developed; P_4 anterior accessory cusp small; P_4 talonid elongate with two posterior accessory cusps; upper molar conules present; molar trigonids high, paraconid < metaconid < protoconid size, paraconid and metaconid closely appressed forming a closed-V trigonid; bullae unossified; scaphoid, lunar and centrale separate; scapula lacking teres major process and secondary scapular spine.

DISCUSSION: Kretzoi (1945) abandoned the order Carnivora and placed all the Carnivora into two other orders, Feliformia and Caniformia. Kretzoi's Feliformia included only the Nimravidae, Felidae, Megantereontidae, and Machairodontidae; whereas the Miacoidae, Canoidea, and remaining Feloidea (of Simpson, 1945) were placed in the Caniformia. Tedford (1976) considered the Feliformia and Caniformia subordinal divisions of the order Carnivora, and he revised these taxa to include the Pinnipedia within the Caniformia, and all of Simpson's Feloidea within the Feliformia. We agree strongly with a natural division of the Carnivora into two clades and we follow Tedford's (1976) arrangement of the Carnivora. However, we amend his characterizations so as to include all the members of the paraphyletic "Miacididae" with their closest relatives in the appropriate carnivoran suborders.

All feliforms enlarge the parastyle of P^4 over the condition found in the various outgroup taxa. In some groups (e.g., Hyaenidae) the parastyle is extremely enlarged and adds a significant component to the shearing or crushing surface area of the tooth. However, in all cases the parastyle is an elaboration of the basal cingular cusp found in most eutherians, even when the cusp is incorporated in an enlarged shearing blade, as in the sabretoothed felids. Development of a large cusp in a similar topographic position

may occur in some Caniformia, but this is not homologous with the enlarged parastyle cusp of feliforms (see following discussion on the Nimravidae).

Wortman and Matthew (1899) used the presence of a deep vertical notch in the metastyle blade of P^4 in the Viverravidae and Viverridae to distinguish these taxa from contemporary Canidae (including "miacines"). This appears to be a good character uniting the Feliformia, all of which have the deep, vertical, slitlike notch and not the primitive, broader, shallower notch characteristic of other carnivorans, creodonts, and some *Cimolestes* (e.g., *C. magnus*).

The upper and lower third molars are lost in all Feliformia. All of the outgroups examined, as well as early Carnivora (e.g., early Tertiary Caniformia), have the full molar complement of $M_1^1\text{--}M_3^3$ found in primitive Eutheria. The Feliformia reduced the number of molars to $M_1^1\text{--}M_2^2$ early in their phyletic history, as all the known feliforms, beginning in the early Paleocene, have lost M_3^3 . Later, more advanced Caniformia may also reduce their molar numbers in parallel, although this can be hypothesized to have occurred independently in a number of phyletic lineages (e.g., advanced members of the groups "Miacinae," Nimravidae, Canidae, Mustelidae, Procyonidae, etc.).

M^2 is reduced in size and complexity in the feliforms, when compared to the morphology of the second upper molar in the outgroups and primitive caniforms. M^2 is much smaller than M^1 , the tooth is narrow anteroposteriorly, and the metastylar region is very reduced. Again, advanced Caniformia may analogously reduce M^2 as they reduce the size and number of molars at the posterior end of the cheek tooth row. Advanced Feliformia may lose M^2 entirely, and similarly reduce M^1 .

Matthew's (1915) key to the genera of Miacidae introduced another character that supported a bipartite split of the Miacidae. The elongate, oval shape of M_2 distinguished *Didymictis* and *Viverravus* (corresponding to his 1909 Viverravinae) from the remainder of the Miacidae. This character may be defined in more detail as an extreme elongation

of the talonid of M_2 , with talonid length equal to, or greater than, the trigonid length. This results in a narrow, elongate, rectangular or oval outline of the entire tooth crown. The narrow, elongate M_2 talonid and the elongate, oval outline of M_2 are also found in some living viverrids (Feloidea) that retain a well-developed M_2 . In all the outgroups M_2 talonid length is shorter than the trigonid length. The primitive caniforms previously classified in the Miacinae also have the primitive state of an M_2 talonid that is shorter in length than the trigonid, and in some cases the talonid length is extremely reduced. Even in forms that parallel the early feliforms in the loss of M_3 (e.g., *Quercygale*, "*Plesiomiakis*," etc.) the talonid of M_2 is very short and never equal to or greater than the trigonid in length.

There is also an enlargement of the hypoconulid on M_2 in conjunction with the lengthening of the talonid. The hypoconulid of M_2 is primitively a large, high and distinct cusp in all Feliformia, and is developed separately from, and posterior to, the entoconid and hypoconid. The hypoconulid is equal in size to, or larger than, the hypoconid, although the hypoconid retains its primitive large size and robust, conical morphology. The hypoconulid on M_2 of the outgroup taxa is generally smaller than the hypoconid and is not elaborated as a large, distinct cusp; rather it is part of a continuous ridge that encircles the talonid basin and incorporates the cristid obliqua, large hypoconid, hypoconulid, and entoconid. The hypoconulid on M_2 of primitive caniforms is very reduced and forms an indistinct cusp or swelling on the low ridge that surrounds the talonid basin. Even in the few derived caniforms that independently expand and lengthen the talonid of M_2 , such as the Procyonidae, the morphology is different; the hypoconulid is not extremely enlarged concurrently with the talonid lengthening and the "entoconid" is a series of cuspules and cusps along the lingual tooth margin. No such multiplication of cusps is seen in the Feliformia.

The Feliformia includes most of the taxa assigned by Simpson (1945) to the Viverravinae (Miacidae) and to the Feloidea, and by

other workers to the equivalents of these groups. However, a number of taxa are obviously excluded from the Feliformia, as defined in the diagnosis above. These include the Nimravidae (Nimravinae and Hoplophoeninae of de Beaumont), *Plesiomiaceis*, *Quercygale*, and *Oödetes*, which are alternatively assigned to the Caniformia, and are considered later in this study. In contrast, the equivocal genus *Palaeogale* appears to be a feliform, as suggested by Hunt (1974b), rather than a mustelid caniform as proposed by Simpson (1946). Therefore, the Feliformia, as defined here, would include *Protictis*, *Didymictis*, *Ictidopappus*, *Viverravus*, *Simpsonictis*, *Palaeogale*, and the Feloidea (exclusive of the Nimravidae).

Our definition of the Feliformia is partly based on characters presented in the literature by other workers. However, many of these characters were initially used to define the "Viverravinae," and their utility in also characterizing the Feloidea remained unrecognized. By distinguishing between the derived and the primitive characters used by earlier workers, a hypothesis of relationship may be proposed that incorporates the Feloidea and "viverravine Miacidae" on the one hand, and the Canoidea and "miacine Miacidae" on the other, into rigorously defined, monophyletic taxa. The Feliformia comprises both early and late Tertiary taxa of one of the two major carnivoran clades.

DIDYMICTIDA, NEW INFRAORDER

DIDYMICTIDAE, NEW FAMILY

TYPE GENUS: *Didymictis* Cope, 1875a.

DISTRIBUTION: Middle Paleocene to late Eocene.

INCLUDED GENERA: *Didymictis* Cope, 1875a; *Protictis* (Matthew, 1937), including the subgenera *P. (Protictis)* (Matthew, 1937); *P. (Bryanictis)* MacIntyre, 1966; and *P. (Protictoides)*, new subgenus.

DIAGNOSIS: Feliform carnivorans differing from all other Feliformia in the following derived characters— M_2 paraconid extremely, and metaconid moderately, reduced, paraconid much smaller than, or subequal to,

metaconid size; P_4 with a well-developed notch between the anterior accessory cusp and the main cusp; P_4 talonid broad; canines multigrooved.

The members of this family are characterized by a number of additional, primitive characters: P_4 retains a long talonid with at least one well-developed, and possibly a second moderately developed posterior accessory cusp; M_1 metaconid not lower than the low paraconid (as is found in some *Viverravus*, whereas the metaconid is lost in some feloids); molar trigonids with paraconid and metaconid relatively closely appressed, resulting in closed trigonids; molar cristids oblique and talonids basined, not trenchant as in some Viverravidae; M_2 sulcus obliquus deep and basined, rimmed ventrally by a basal cingulum; M_2 hypoconulid large, lingual, closely appressed to entoconid, as opposed to the relatively larger hypoconid of caniforms and the posterocentral hypoconulid, well separated from the entoconid, found in the Viverravidae and *Ictidopappus*; conules on the upper molars always present and well developed, not lost as in all other Feliformia; cingulae well developed, except in *P. (Protictoides)*, in contrast to weak cingular development in other feliforms.

DISCUSSION: This family is proposed for the members of one branch of the Feliformia that remain conservative in most of their dental and skeletal morphology, but that are united by a number of derived features. We follow MacIntyre (1966) in recognizing Matthew's subgenus *Didymictis* (*Protictis*) as a distinct genus, with the morphologically distinct subgenera *P. (Protictis)* and *P. (Bryanictis)*. We exclude MacIntyre's subgenus *P. (Simpsonictis)* from *Protictis* and the Didymictidae, and include it as a resurrected genus in the Viverravidae (see below). We do not follow Rigby's (1980) suggestion that *Bryanictis* be generically differentiated from *Protictis*, as our analysis has clearly shown that the two taxa share a number of derived features and are best considered members of the same genus (see below). We also propose a new subgenus *P. (Protictoides)* from the middle Eocene of Wyoming.

Both *Didymictis* and the various subgenera of *Protictis* share a number of specialized dental characters that unite them in a monophyletic group, for which we propose the name Didymictidae. The distinctive taxon of primitive carnivoran perceived by early workers in their broadly constructed, paraphyletic grouping of species within *Didymictis* is retained in the usage of a family Didymictidae, whereas the diversity and monophyletic nature of the included material is still recognized in the taxonomic distinction of the various included genera and subgenera. We also propose a new taxon, the infraorder Didymictida, that includes only the members of the family Didymictidae. This higher level taxon represents a group of equivalent rank to the Aeluroidea (see below), and we favor its use to differentiate one major evolutionary branch of the Feliformia. The diversity represented within the Didymictida is much less than in the Aeluroidea, but it is clear that the two taxa represent a fundamental, dichotomous split in the phylogenetic history of the Feliformia.

The Didymictidae are generally primitive members of the Feliformia, except for the few derived characters discussed below. The family represents an early offshoot from the feliform stock that evolved certain autapomorphies in the various included taxa, but that largely remained primitive in both the skeleton and the dentition. *Protictis* (*Protictoides*) represents the last occurrence of the family in the earliest Uintan, and the group has no close living descendants in the modern carnivoran fauna.

The paraconid of M_2 is extremely reduced in the Didymictidae, whereas the metaconid is more moderately reduced. This results in a very low M_2 trigonid, with poorly distinct paraconid and metaconid cusps. The trigonid is much lower than that found primitively in feliforms and represents a reduction in both talonid height and cusp development over the primitive state for Carnivora. Other feliforms retain the primitive condition of a moderately high trigonid and well-developed cusps, with the paraconid lower than the metaconid, except in those Felioidea that

reduce, or lose entirely, M_2 . In *Didymictis* the trigonid is lower than in other Didymictidae and the trigonid cusps are extremely reduced.

All Didymictidae develop a distinct, narrow, deep carnassiform notch between the anterior accessory cusp and the main cusp on P_4 . The notch in didymictids is deeply excavated and V-shaped, and the anterior accessory cusp is closely appressed to the main cusp. The anterior cusp may remain small, primitively, but the notch is clearly elaborated in all included taxa. Other feliforms lack this notch, as the anterior accessory cusp is well separated and offset lingually from the main cusp by a wide, shallow, U-shaped valley.

The talonid of P_4 in the didymictids is broadened over the primitive state for feliforms, although the two posterior accessory cusps and the posterior talonid cingulum characteristic of all Carnivora is retained. The increase in transverse talonid width occurs largely in the lingual portion of the talonid; the talonid basin is enlarged, deepened, and rimmed lingually by a higher lateral wall. No other feliforms or caniforms develop such a broad, deep, basined talonid on P_4 .

The canines are multigrooved in the only Didymictidae for which they are known, *P. (Protictis)* and *Didymictis*. Grooving of the canines may be derived for the Didymictidae, as it is not present in *Viverravus*. However, the distribution of this character may be biased by the lack of preserved canines in many early feliforms, and it is possible that grooved canines are primitive for the Feliformia. The grooving exhibited in the Didymictidae is a multiple series of closely spaced, deep grooves extending along the entire height of the tooth crown, and most deeply excavated near the base of the crown. Similar grooving may be found in some Felioidea, but is not present in any of the outgroups. Therefore, the polarity of this character is uncertain.

Didymictis is derived in a number of features, including: reduction of P_4 posterior accessory cusps to one; close appression of the paraconid and metaconid on the lower

molar trigonids; great elaboration of cheek teeth basal cingulae; and reduction of M_2 trigonid.

The talonid of P_4 remains elongate in *Didymictis* but the number of posterior accessory cusps and notches is reduced to one.

Didymictis modified its trigonids quite differently from all other feliforms, through extremely close appression of the paraconids and metaconids, ultimately resulting in near fusion of the two cusps in extremely derived species (e.g., *D. protenus*).

Didymictis elaborated on the cingulae primitively present in this group, and evolved extremely pronounced basal cingulae rimming the cheek teeth. The cingulae became very broad and developed numerous rugosities and cusplules that are very distinctive features of this genus.

The *Didymictis* lineage evolved toward larger size and greater occlusal surface area on the cheek teeth. This was achieved by an increase in the area, length, and crenulation of the cingular enamel, as well as a reduction in the trigonid height and cusp development of M_2 . This resulted in a nearly continuous, flat, platelike surface extending from the base of the M_1 trigonid to the posterior margin of the M_2 talonid, and is found in *Didymictis* only.

PROTICTIS (MATTHEW, 1937)

TYPE SPECIES: *Protictis (Protictis) haydenianus* (Cope, 1882).

INCLUDED SUBGENERA: *Protictis (Protictis)* Matthew, 1937; *P. (Bryanictis)* MacIntyre, 1966; and *P. (Protictoides)* new subgenus.

DISTRIBUTION: Middle Paleocene to middle Eocene.

DIAGNOSIS: Members of the Didymictidae differing from other taxa included in the family by the following derived features— anterior accessory cusp on P_4 enlarged and very high; lingual margin of P_4 straight anteroposteriorly, not curved; P^3 develops a weak, but distinct, protocone cusp anterior to the apex of the paracone; P_4 main cusp situated on the buccal tooth margin; main cusp on P_4 leaf-shaped in outline.

Protictis also differs from *Didymictis* in

the features characterizing the latter genus. These features in *Protictis* include: lack of extremely well-developed cingulae on the cheek teeth; M_2 paraconid and metaconid not so extremely closely appressed; M_2 trigonid higher; retention, primitively, of two posterior accessory cusps on the talonid of P_4 .

Protictis (Protictis) differs from all other *Protictis* in: extremely narrow M_2 talonid; transversely narrow, elongate parastyle lobe on P^4 ; strong "backward tilting" of paracone, and straight, vertical posterior margin of paracone on P^4 ; first posterior accessory cusp located vertically high on posterior flank of main cusp on P_4 .

DISCUSSION: Matthew's (1937) recognition that "*Didymictis*" (*Protictis*) represented a clearly distinct, morphologically definable taxon within *Didymictis* was an essential step in the separation of monophyletic taxa from a diverse paraphyletic assemblage.

In 1966 MacIntyre formally designated a new genus, *Protictis*, for the material included within Matthew's subgenus. Most of the characters used to define and describe the taxa included here in *Protictis* are well described and illustrated in MacIntyre's paper, and that study should be consulted for a more detailed analysis of the morphology of these groups.

MacIntyre's (1962) recognition of the unique morphology represented by Simpson's (1935) "*Didymictis*" *tenuis* also added to our knowledge of the diversity present early in carnivoran evolution. However, we believe that MacIntyre's initial decision to provide generic status for *Simpsonictis tenuis* is valid, and we therefore do not follow his latest (1966) inclusion of *Simpsonictis* as a subgenus of *Protictis*. Rigby (1980) and Van Valen (1969) have resurrected *Simpsonictis*, and we agree with this action. We do so, however, because the members of the taxon lack the diagnostic, derived features of *Protictis* and the Didymictidae, and instead share derived features with *Viverravus*. *Simpsonictis* is an unusual, derived, early Tertiary member of the Feliformia that is generically separable from all other carnivorans and is closely related to *Viverravus*,

rather than *Protictis* (as suggested by Rigby and MacIntyre, in Rigby, 1980).

As mentioned previously, we do not agree with Rigby (1980) that *P. (Bryanictis)* represents a genus distinct from *Protictis (Protictis)*. There are a number of features that exclusively ally the two taxa, as will be elaborated below, and nothing to support a generic separation of the two. Rigby does not provide a new diagnosis that would serve to differentiate *P. (Bryanictis)* at the generic level. *Protictis (Protictis)* and *P. (Bryanictis)* are very closely related, and without better evidence for an alternative hypothesis of relationship, we see no reason for separating *P. (Bryanictis)* as a new genus.

Protictis is a distinctive, monophyletic taxon within the Didymictidae. All the taxa included within *Protictis* greatly enlarge the size of the anterior accessory cusp on P_4 . This cusp becomes high and is clearly derived over the small, low anterior accessory cusp characteristic of the Feliformia, Caniformia, and all the Cretaceous outgroups. In connection with the enlargement of the cusp, the notch between the anterior accessory cusp and the main cusp becomes much deeper than the notch in *Didymictis*.

The main cusp on P_4 is situated far buccally, along the buccal edge of the tooth. The entire cusp row is thus aligned in a smooth arc, convex buccally, and is located close to the buccal margin of the tooth. The buccal margin of the tooth is also smooth and continuous, and is buccally convex. This contrasts with the primitive morphology exhibited by *Didymictis*. In *Didymictis* the main cusp is on the lingual edge of the tooth crown. The cusp row does not form a continuous, smooth line or arc, and the outline of the buccal margin of the tooth is interrupted by a number of bulges and constrictions along its anteroposterior length. In the Aeluroida, there are constrictions of the crown at the bases of all the cusps on P_4 , and lateral bulgings where the cusps are the most robust. The cusps are not arranged in a linear or arcuate manner, and they tend to lie at the center or lingual portion of the crown. The lingual margin of P_4 in *Protictis* is derived in its anteroposteriorly straight

occlusal outline, uninterrupted by constrictions or expansions of the lingual tooth crown. This suite of characters results in a P_4 in *Protictis* that has an extremely smooth occlusal outline, a wide area of lingual basining and broad sloping off the shoulders of the cusps, and a steepening of the buccal tooth crown.

All the species of *Protictis* that preserve P^3 show the development of at least a weak protocone cusp located anterior to the paracone. *Protictis* is the only feliform that develops a protocone on P^3 . Other Carnivora have a well-developed cingulum on the posterolingual margin of P^3 , at the base of a deep, lingual paracone slope or shelf. *Protictis* develops a distinct cusp at the anteriormost edge of this lingual cingulum, thereby broadening P^3 and adding another lobe to the tooth. The protocone is anterior to the apex of the paracone in all cases. The polarity of this character is debatable, as some of the Cretaceous outgroups have a protocone on P^3 , although it is not anterior to the apex of the paracone (see discussion on Carnivora above). If the presence of a protocone on P^3 is primitive, then all other feliforms and the caniforms must have lost it independently, while *Protictis* remained primitive in its retention of this cusp. Based on the arguments given previously, however, we regard the presence of an anteriorly positioned P^3 protocone as uniquely derived for *Protictis*. The development of a distinct, lingual protocone cusp may be correlated with the elaboration of the anterior accessory cusp on P_4 , as these two cusps would provide complementary occlusal surfaces for increased shear.

The species included within *Protictis* all possess a main cusp on P_4 that is anteroposteriorly constricted on its anterior and posterior flanks. This constriction occurs about midway up the height of the cusp, at the notches that mark the junctions between the main cusp and the anterior and first posterior accessory cusps. As a result of this constriction, the main cusp has a "leaf-shaped" outline in lateral view. This is derived with respect to the primitive, inverted-V shaped main cusp found on P_4 in other Carnivora and eutherian outgroup taxa.

MacIntyre's (1966) diagnosis of *Protictis* (*Protictis*) indicated that the talonid of M_2 in this subgenus was relatively much narrower than in any other early Tertiary feliform. *Protictis* (*Bryanictis*) and taxa which serve as outgroups to the *Protictis* clade (e.g., *Didymictis* and the Caniformia) all have a much wider M_2 talonid. Therefore, this feature distinguishes *P.* (*Protictis*) from all other *Protictis*.

The parastyle lobe of P^4 in *P.* (*Protictis*) is very narrow transversely and is elongated in an anterobuccal/posterolingual direction. This results in an elongate, oval outline for the parastyle lobe and cusp that differs from the shape found in all other carnivorans. *Didymictis*, *P.* (*Bryanictis*), *P.* (*Protictoides*), and *Viverravus* all have a more rounded and conical shape for this lobe; in the Caniformia, however, the parastyle cusp and lobe are extremely small or absent.

Protictis (*Protictis*) has an extremely straight, vertically oriented posterior margin on the paracone of P^4 . The anterior slope of the paracone is long and extends far posteriorly to the paracone apex. This results in a paracone profile that points posteriorly and appears to be "tilting" in a posterior direction. The paracone apex is relatively farther anterior, and the anterior paracone slope is shorter, in all other *Protictis*, *Didymictis*, and early Tertiary Carnivora.

The first posterior accessory cusp on P_4 of *P.* (*Protictis*) is positioned very high on the posterior flank of the main cusp. This cusp is higher in *P.* (*Protictis*), relative to the base of the tooth crown and the talonid rim, than in any other early Tertiary carnivoran.

PROTICTIS (*BRYANICTIS*) MACINTYRE, 1966

TYPE SPECIES: *Protictis* (*Bryanictis*) *microlestes* (Simpson, 1935).

INCLUDED SPECIES: *P.* (*Bryanictis*) *microlestes* (Simpson, 1935) and *P.* (*B.*) *vanvaleni* MacIntyre, 1966.

DISTRIBUTION: Middle and ?late Paleocene.

DIAGNOSIS: Members of the genus *Protictis* that share all the derived characters of that genus, but that differ from all other *Pro-*

tictis in the following derived features— P_4 anterior accessory cusp tremendously enlarged and modified for shearing; expansion and very deep basining of the lingual portion of the talonid of P_4 ; large, well-developed P^3 protocone; all P_4 cusps very strongly laterally compressed; alignment of the cusps on P_4 in a straight, anteroposterior line on the buccal tooth margin, buccal margin of the tooth straight anteroposteriorly, or only slightly convex buccally.

DISCUSSION: MacIntyre's (1966) diagnosis and description of this subgenus, and its included species, provides the most comprehensive treatment of this taxon. Our diagnosis is presented only to elaborate on the derived morphology present in this subgenus, and as evidence to document the monophyletic nature of *P.* (*Bryanictis*). Both *P.* (*B.*) *microlestes* and *P.* (*B.*) *vanvaleni* share derived characters that ally them more closely to each other than to any other taxon, which strongly supports the validity of retaining these two species within their own distinct subgenus. The arguments for not considering these species as members of a distinct genus have been given above.

Most of the characters used to ally *P.* (*B.*) *microlestes* and *P.* (*B.*) *vanvaleni*, are shared in a more primitive condition by all *Protictis*. *Protictis* (*Bryanictis*) elaborated greatly on these features and evolved a morphology that is more derived than that exhibited by other *Protictis*. The protocone on P^3 of *P.* (*Bryanictis*) is greatly enlarged and forms a distinct, bulbous, high cusp on a lingual lobe of P^3 . The protocone is larger, better developed as a distinct cusp, and invariably present in this subgenus, as opposed to the more variable intraspecific presence and smaller size of this cusp on P^3 in *P.* (*Protictis*) *haydenianus*. The protocone is well anterior to the apex of the paracone, as in *P.* (*Protictis*). P^3 is unknown in *P.* (*B.*) *vanvaleni* and *P.* (*Protictoides*).

The anterior accessory cusp on P_4 in both species of *P.* (*Bryanictis*) is elaborated into a large, vertical shearing blade at the anterior end of the tooth. As mentioned in the discussion of *Protictis*, the enlargement of the anterior accessory cusp appears to be cor-

related with an increase in the size of the protocone of P^3 . This certainly seems to be the case in *P. (Bryanictis)*, as both the protocone of P^3 and the anterior accessory cusp on P_4 are greatly enlarged and would have acted as an efficient shearing pair during occlusion. The very deep, narrow, carnassiform notch on P_4 , between the anterior accessory cusp and the main cusp, would also have been involved in the increased shear between P^3 and the anterior part of P_4 . The anterior accessory cusp of P_4 in *P. (Bryanictis)* is unique among feliforms, in that it is much taller than the first posterior accessory cusp. Even in other *Protictis*, in which the anterior accessory cusp is also enlarged, the anterior cusp height is never greater than the height of the apex of the first posterior cusp. In all *Protictis* species, however, as in all other carnivorans, the main cusp on P_4 is always the tallest and dominates the tooth crown.

All the cusps on P_4 in *P. (Bryanictis)* are very strongly laterally compressed. This is particularly extreme in *P. (B.) vanvaleni*, in which the cusps are very thin transversely and the flanks of the cusps are nearly vertical. This results in an extremely sharp, narrow, continuous ridge on the buccal tooth margin, that runs the entire length of the tooth and connects the crests of the cusps.

The alignment of P_4 cusps in *P. (Bryanictis)* is derived over the primitive condition for *Protictis*; the cusps are aligned straight anteroposteriorly along the extreme buccal margin of the tooth. This contrasts with the more arcuate arrangement of the cusps on the crown in other *Protictis*. The cusp row in *P. (Bryanictis)* forms a very straight, high wall on the buccal tooth margin, bordering a wide surface area on the lingual side of P_4 . In outline, the buccal margin of the tooth crown is also smooth and straight anteroposteriorly, or only slightly convex buccally. The buccal tooth margin in *Protictis* is also smooth, although it is much more strongly buccally convex, whereas the crown outline in *Didymictis* is very irregular in shape with numerous constrictions and expansions of the margin.

A transverse expansion and deep basining

of the lingual portion of the talonid of P_4 is a derived feature for both species of *P. (Bryanictis)*. This is a greater elaboration of the condition found in other *Protictis*, in which the talonid is moderately wide and basined. The talonid basin of P_4 in *P. (Bryanictis)* is extremely wide and deep and is entirely encircled by a high basin rim. The rim is composed of the posterior accessory cusp wall buccally, and a high cingulum on the posterior and lingual margins of the tooth. The deep basining is best developed on P_4 of *P. (B.) vanvaleni*.

PROTICTIS (PROTICTOIDES), NEW SUBGENUS

TYPE SPECIES: *Protictis (Protictoides) aprophatos*, new species.

INCLUDED SPECIES: The type species only.

DISTRIBUTION: Earliest Uintan (middle Eocene).

ETYMOLOGY: Subgeneric name from a combination of the Greek *-oides*, meaning like or resembling, and *Protictis*; in reference to the morphological similarity and hypothesized close phyletic relationship to *Protictis (Protictis)*.

DIAGNOSIS: Member of the genus *Protictis*, differing from all other *Protictis* in the following derived features— P^4 anterior margin extremely straight, not embayed; P^4 cingulae very reduced or absent; P^4 labial margin straight; P^4 occlusal outline triangular, with all borders straight; P_4 cingulae reduced or absent; P_4 with very strong, high posterior transverse talonid ridge (cingulum).

CHARACTERIZATION: The known elements, P^4 and P_4 of *P. (Protictoides) aprophatos* approximate the size of late Paleocene *Didymictis*. *Protictis (Protictoides)* greatly exceeds the size of *Simpsonictis*, *P. (Bryanictis)*, *P. (Protictis)* and *Viverravus* (see table 2). The presence of an extremely large, trenchant P^4 parastyle and protocone (see fig. 5) clearly distinguishes *P. (Protictoides)* from *P. (Bryanictis)*, *P. (Protictis)*, *Didymictis* and *Viverravus*. The basined area labial to the protocone, between the paracone and the parastyle, is much broadened. The labial base of the paracone is con-

TABLE 2
Measurements (in Millimeters) of Early Tertiary Feliformia

Data on *Protictis* (*Protictis*), *Protictis* (*Bryanctis*), *Ictidopappus*, and *Simpsonictis* from MacIntyre, 1966

	P ⁴ length, labial	P ⁴ metastyle (length)	P ⁴ length, lingual	(P ⁴) premolar width	(P ₄) premolar length	(P ₄) premolar width
<i>P. (Protictis) haydenianus</i> (Torrejonian localities, New Mexico)	7.77 ± 0.12	2.70 ± 0.10	9.22 ± 0.09	5.85 ± 0.19	6.95 ± 0.09	3.16 ± 0.03
<i>P. (Protictoides) aprophatos</i> (Wind River Basin, Wy- oming)	12.86	4.48	14.29	8.39	8.86	3.91
<i>P. (Bryanctis) microlestes</i> (Gidley Quarry, Montana)	4.86 ± 0.07	1.73 ± 0.06	5.98 ± 0.13	3.72 ± 0.05	4.31 ± 0.06	2.03 ± 0.04
<i>P. (Bryanctis) vanvaleni</i> (Torrejonian, New Mexico)					4.6	2.35
<i>Ictidopappus mustelinus</i> (Gidley Quarry, Montana)	5.0	2.7	5.1	3.7	3.0	2.0
<i>Simpsonictis tenuis</i> (Gidley Quarry, Montana)					2.48 ± 0.07	1.12 ± 0.02
<i>Viverravus gracilis</i> (genotype) (Bridger Basin, Wyoming)	6.13	2.43	6.95	3.70	5.61	1.93
<i>Viverravus sicarius</i> (type) (Bridger Basin, Wyoming)	9.22	3.41	9.99	6.12	7.69	3.34

vex, rather than concave, giving P⁴ a straighter occlusal profile than that found in the above mentioned genera. The anterior and lingual margins of the tooth are also extremely straight, resulting in a strongly triangular occlusal outline. The basal cingulum is very weakly developed, being most pronounced at the lingual base of the metastyle and at the anterolabial base of the paracone. The metastyle blade is elongated anteroposteriorly into a well-developed, straight shearing crest. All the cusps are laterally compressed into trenchant piercing points and ridges, rather than bulbous and rounded as in *Didymictis* and *Viverravus*.

P₄ retains the primitive condition of a well-developed second posterior accessory cusp distinct from the posterior cingular ridge. This differs from the talonid structure of P₄ in *Simpsonictis*, *Didymictis*, *Ictidopappus*, and *Viverravus* which have reduced the second posterior accessory cusp. It is similar,

however, to the unmodified condition also found in *P. (Protictis)*, *P. (Bryanctis)* and various "miacines" in which the presence of a second posterior accessory cusp creates a notch between this cusp and the more anteriorly located first posterior accessory cusp. The anterior accessory cusp, although proportionally smaller than in *P. (Bryanctis)*, is stronger and positioned closer to the main cusp than in *Simpsonictis*, *Viverravus*, and *Didymictis*. It most closely resembles *P. (Protictis)* in this feature. The cusps are transversely compressed and have a leaf-shaped outline in lateral view, similar to the condition in *P. (Protictis)*, *Didymictis*, and the extreme elaboration found in *P. (Bryanctis)*. The basal cingulum is extremely weak on P₄, with significant development only on the posterior border of the tooth where it forms a pronounced, buccolingual ridge behind the second posterior accessory cusp.

The comparative description provides ad-

ditional details and elaboration on diagnostic characters of *P. (Protictoides) aprophatos*.

Protictis (*Protictoides*) aprophatos,
new species
Figures 2, 3, 5, 6

HOLOTYPE: AMNH 97701; isolated right P^4 .

TYPE LOCALITY: Bone Bed A of Love (1939), type section of the Tepee Trail Formation, East Fort Basin, 17 miles northeast of Dubois, northwest portion of the Wind River Basin, Fremont County, Wyoming.

AGE: Earliest Uintan (middle Eocene—see McKenna, 1980; Berggren et al., 1978).

DIAGNOSIS: Same as for the subgenus.

ETYMOLOGY: Species name from the Greek *aprophatos*, meaning unfortold or unexpected; in reference to the unusual occurrence of a species of *Protictis* in the Uintan (middle Eocene).

REFERRED MATERIAL: AMNH 105371, right ramal fragment bearing P_4 and the alveolus for the posterior root of P_3 . Also from Bone Bed A, and possibly belonging to the same individual as the holotype.

Association of P^4 and P_4 : The assignment of the two Tepee Trail specimens to the same species is unquestionable. Both specimens were discovered in the same locality and perfectly complement each other in size. They occlude well with one another, indicating a possible individual association as well, although this cannot be determined with certainty.

The poor dental representation of *P. (Protictoides) aprophatos* is compensated by the fact that these two teeth are quite diagnostic carnivoran elements. P_4 's in carnivorans exhibit great diversity at all taxonomic levels. The striking morphologic differences seen in *P. (P.) aprophatos* are considered diagnostic at the subgeneric level. As detailed in later sections, the characters analyzed do not intergrade (form part of a variability sequence) with those of other carnivoran genera. The derived nature of many of the characters in *P. (Protictoides)* tends to further emphasize the distinction of the Tepee Trail form from other carnivorans.

COMPARATIVE DESCRIPTION

Comparison to other primitive feliforms:

(1) P^4 : The protocone of P^4 in *P. (Protictoides) aprophatos* is broad, stands high, and is so prominent as to create a sharp drop immediately posterolabial to the cusp (where the anteromedian edge of the paracone and the protocone meet). The summit projects upward almost as high as the metastyle, when viewed from the medial side and when the base of the crown is placed horizontally (see fig. 5). This strongly contrasts with P^4 protocone morphology in the "miacine" genera *Miacis*, *Uintacyon*, *Vassacyon*, *Vulpavus*, *Procynodictis*, and *Tapocyon* in which the protocone is small, bulbous, low crowned, and noticeably lower than the metastyle. The *P. (Protictoides)* protocone morphology is similarly exhibited in *P. (Bryanictis)*, *Viverravus*, *P. (Protictis)*, and *Didymictis*, but in these genera the relative height of the protocone to the height of the parastyle is less when compared to *P. (Protictoides)*. The protocone of P^4 in *P. (Protictoides)* is more trenchant than in *Didymictis*. In *Didymictis* and *P. (Bryanictis)* the protocone is more rounded and bulbous than in *P. (Protictis)* (based on AMNH 17059) and *P. (Protictoides) aprophatos*. *Protictis (Protictis)*, *P. (Bryanictis)*, *Viverravus*, and *Didymictis* all have a strong, distinct cingulum rimming the base of the crown, as opposed to the very weak cingulum development in *P. (Protictoides) aprophatos*.

The occlusal surface labial to the protocone, between the paracone and parastyle (area of P_4 talonid occlusion) is proportionally much more expanded on P^4 in *P. (Protictoides)* than in *P. (Bryanictis)*, *P. (Protictis)*, *Didymictis* and *Viverravus*. In occlusal view, the anterolingual portion of the paracone in *P. (Protictoides) aprophatos* appears to be more convex than in the above genera, thereby filling out the indentation between the parastyle and the protocone.

The parastyle of *P. (Protictoides) aprophatos* (as in *P. (Bryanictis)*, *P. (Protictis)* and *Viverravus*) lacks the cingulum encircling the base of the cusp that is found in *Didymictis*. However, a faint cingulum orig-

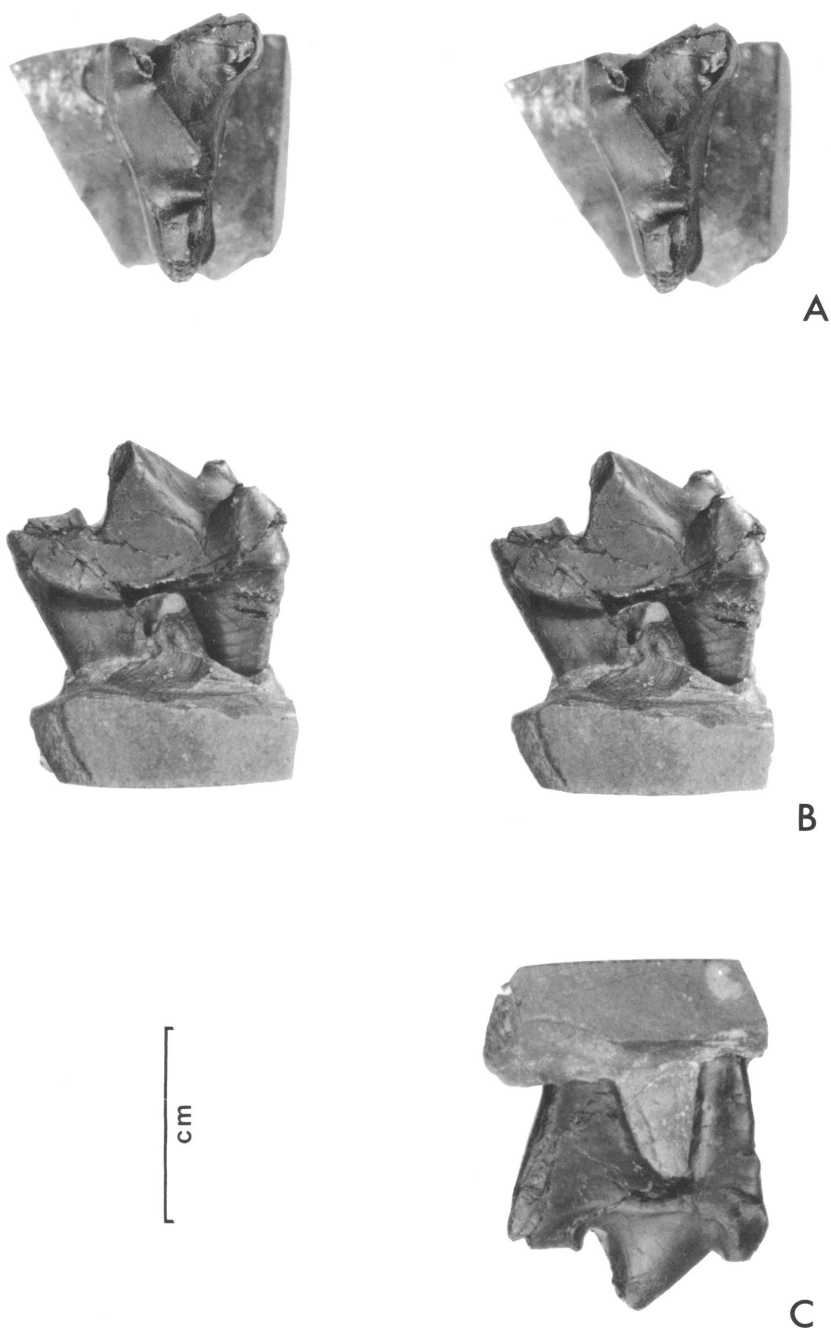


FIG. 5. *Protictis (Protictoides) aprophatos*, AMNH 97701, type specimen, right P⁴. Stereophotographs of occlusal (A) and lingual (B) views. Photograph of labial (C) view. Anterior direction toward top of page in A, and toward right of page in B and C. Scale is 1.0 cm.

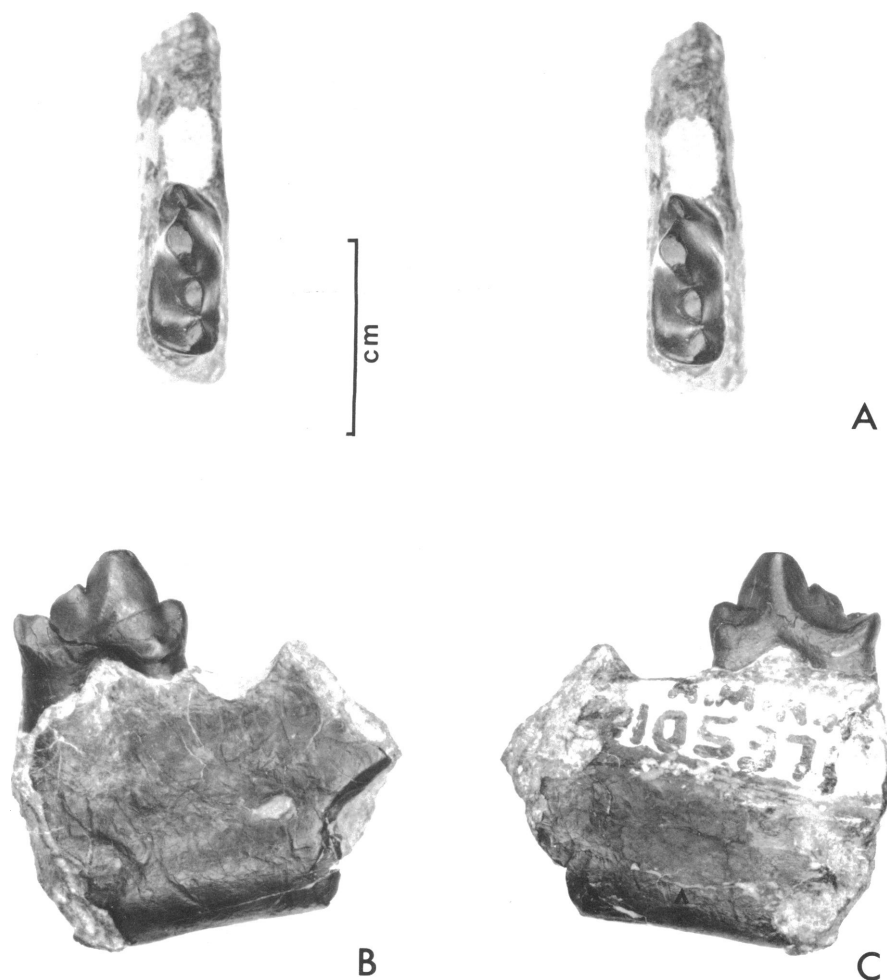


FIG. 6. *Protictis (Protictoides) aprophatos*, AMNH 105371, referred specimen, right P_4 and partial mandible. Stereophotographs of occlusal (A) view. Photographs of labial (B) and lingual (C) views. Anterior direction toward top of page in A, right of page in B, and left of page in C. Scale is 1.0 cm.

inates at the posterolabial base of the parastyle, runs along the labial margin of the tooth, and terminates at the metastyle. This condition of the cingulum is similar to that seen in *P. (Bryanictis)*, *P. (Protictis)* and *Viverravus*. Proportionate to the protocone, the parastyle is much stronger and taller in *P. (Protictoides)* than in *P. (Bryanictis)*, *Viverravus*, and *Didymictis* (the parastyle in *Didymictis* is short and bulbous). The para-

style of P_4 in *P. (Protictis)* is proportioned similarly to that in *P. (Protictoides)*. The large, deeply notched P_4 parastyle is unique to *P. (Protictoides)* and is not found in any other North American Eocene carnivoran genus.

The lingual and labial cingulae of P_4 in *P. (Protictoides) aprophatos* are faint. This condition more closely resembles the cingular development found in *P. (Bryanictis)*, *P.*

(*Protictis*), and *Viverravus* than that observed in *Didymictis*, which has distinctly stronger cingulae. The enamel at the base of the protocone in AMNH 97701 is slightly damaged, making it difficult to determine the extent of the lingual cingulum in *P. (Protictoides)*. The cingulum begins at the metastyle, but it does not appear to have encircled the protocone as clearly as in *Didymictis*.

In occlusal view, the base of the paracone on P^4 in *P. (Protictoides)* projects more labially than in *P. (Bryanictis)*, *P. (Protictis)*, *Didymictis*, and *Viverravus*. On both sides of the paracone/metastyle notch in AMNH 97701 the edges of the shearing ridge are damaged, making comparisons of the height and wear of that area of P^4 to other taxa difficult.

(2) Ramus and P_4 : A mental foramen is present beneath the alveolus of the posterior root of P_3 in the referred ramal fragment of *P. (Protictoides) aprophatos*. Comparison shows that a mental foramen may be located in the area below P_3 in most primitive carnivorans. The ramal fragment is somewhat narrow transversely and slender as compared to the deep and thick jaws of *Tapocyon*, *Uintacyon*, *Vassacyon*, and *Vulpavus*. The ramal proportions are similar to those observed in *Viverravus*. This suggests that the Tepee Trail form may have been rather long-snouted with an uncrowded premolar dentition.

P_4 is practically undamaged, with slight to moderate oblique wear on all the cusps (similar to the degree of wear observed in the upper carnassial). The anterior cusp is proportionally larger, and positioned closer to the primary cusp, than in *Didymictis*. *Viverravus*, *Didymictis*, and *Simpsonictis* have relatively small anterior accessory cusps on P_4 when compared to those of *P. (Protictis)*, *P. (Protictoides)*, and *P. (Bryanictis)* (the cusp is relatively largest in the last two genera). The lateral profile of the primary cusp on P_4 in *P. (Protictoides)* becomes constricted anteriorly and posteriorly at the notches between this cusp and the anterior and first posterior accessory cusps. Both species of *P. (Bryanictis)*, and to a lesser degree *P. (Protictoides)* and *P. (Protictis)*, share this

rather leaf-shaped primary cusp. As in *Viverravus*, *Didymictis*, *P. (Protictis)*, and *Procynodictis* the first posterior accessory cusp of P_4 in the Tepee Trail specimen stands significantly taller than the anterior accessory cusp. The opposite condition is found in *Tapocyon* and *P. (Bryanictis)*, in which the anterior accessory cusp of P_4 is slightly taller than the first posterior accessory cusp. The first posterior accessory cusp in *P. (Protictis)* and *P. (Protictoides)* does not dominate the talonid, nor is it positioned as low as in *Didymictis* or *Viverravus*. Instead, it is in positional alignment with the second posterior accessory cusp, and is positioned higher on the tooth crown. In *P. (Protictis)* the P_4 first posterior accessory cusp is proportionally smaller, relative to the talonid size, than that of *P. (Protictoides)*. The posterior region of the talonid is dominated by two features in *P. (Protictoides)*: a small, but distinctly developed second posterior accessory cusp, and an internally broad, high, ridge-forming posterior cingulum, which together occupy an area equal to that covered by the first posterior accessory cusp. The second posterior accessory cusp and the posterior cingulum form the margins of a well-developed, concave lingual basin. The strong development of both the first and second posterior accessory cusps results in the formation of a second, distinctive, deep and elaborate talonid notch, a feature that is similarly developed in *P. (Protictis)*.

A posterior labial cingulum is barely observable on the *P. (Protictoides)* P_4 , which is similar to the condition of the cingulum in *Viverravus* and *P. (Bryanictis)*.

The *Ictidopappus* P^4 is very autapomorphic and differs from *P. (Protictoides) aprophatos* in the following features: its much smaller size; protocone located medial to the paracone rather than the parastyle; absence of a basin between the protocone, parastyle and paracone; paracone lower; a "wavy" buccal tooth margin; total lack of cingulae; less distinct, more trenchant cusps; better developed shear facets; less distinct paracone-metastyle blade notch; and more deeply embayed anterior margin.

The *Ictidopappus* P_4 is also very derived

and differs from *P. (Protictoides)* in: its much smaller size; lack of talonid development; straight anterior and posterior edges of the main cusp, in profile; lack of a notch between the anterior accessory cusp and the main cusp; weak posterior, transverse, cingular talonid ridge; larger main cusp; subtriangular, rather elongate-rectangular, occlusal outline.

P_4 in *Simpsonictis* differs from *P. (Protictoides)* by: its much smaller size; anterior accessory cusp lower and more anteriorly located; first posterior accessory cusp much smaller and lower on the base of the main cusp; main cusp relatively higher; tooth less elongate and rectangular; talonid less broad; lingual talonid basin less well developed; lack of the second posterior accessory cusp and notch.

Comparison to Uintan caniforms:

*Miacis*⁷ lacks a prominent parastyle, has a proportionally smaller P^4 protocone, has relatively weaker and less distinct posterior accessory cusps on P_4 , has a deeper ramus beneath P_4 , and averages smaller in size than *P. (Protictoides) aprophatos*.

In *Uintacyon* and *Vassacyon* the depth of the mandible below P_4 is proportionally much deeper, the talonid of P_4 is never as large, and the protocone and parastyle of P^4 are never so large and trenchant as in *P. (Protictoides)*. A significant feature distinguishing *P. (Protictoides)* from *Uintacyon* and *Vassacyon* is the lack of the second posterior accessory cusp and talonid notch in the latter, but the retention of the primitive state in *P. (P.) aprophatos*.

The broadened protocone, absence of a

parastyle, short metastyle blade, concave labial margin and moderately well-developed cingulae on the *Prodaphaenus* P^4 quickly differentiate it from *P. (Protictoides)*. The teeth in *Prodaphaenus* appear to be generally adapted for omnivory, as opposed to the dentition in *P. (Protictoides)* which seems best suited for hypercarnivory.

The general arrangement and proportions of the cusps on P_4 in *P. aprophatos* are most similar to the morphology found in *Procynodictis* (including *Plesiomiaccis*, see below). *Protictis (Protictoides)* differs from *Procynodictis* in its much larger size; the large size of the anterior accessory cusp on P_4 ; the lack of cingulae on P_4 ; the development of a strong, transverse posterior talonid ridge; and the more shallow depth of the jaw beneath P_4 . In addition, the structure of P^4 is extremely different between *P. aprophatos* and *Procynodictis* in that the latter lacks a parastyle and has a very reduced protocone.

Tapocyon differs from *P. (Protictoides)* in its more reduced and less trenchant protocone, smaller parastyle, and shallower carnassial notch on P^4 and its lack of a second posterior accessory cusp on P_4 . *Tapocyon* is similar, however, in the development of a large anterior accessory cusp on P_4 .

AELUROIDA, NEW INFRAORDER

INCLUDED TAXA: *Ictidopappus*, the Viveravidae, *Palaeogale*, and the Feloidea.

DISTRIBUTION: Early or middle Paleocene to Recent.

DIAGNOSIS: Members of the Feliformia which differ from all other feliforms in the following derived features—conules absent on all upper molars; M_1 paraconid and metaconid distantly separated, resulting in an open-V on the trigonid of M_1 ; loss of the second posterior accessory cusp on P_4 , talonid simpler; reduction of molar cingulae.

The Aeluroida primitively retain the following feliform characters that are modified in the other Feliformia, the Didymictida: P_4 anterior accessory cusp very small and well separated from the main cusp by a broad, U-shaped valley; P_4 talonid relatively narrow and shallowly basined or with lingually slop-

⁷ Simpson (1945) placed the genus *Mimocyon* Peterson, 1919 in *Miacis*. We disagree with this synonymy. The holotype of *Mimocyon longipes* is neither *Miacis*, nor even a carnivoran. This late Uintan form is extremely similar to the Bridgerian hyaenodontid species *Proviverra (?) major* Wortman, 1902 (see Matthew, 1909, p. 473, pl. XLV, fig. 4), but is much larger and has a slightly larger posterior cusp on P_4 . Thus, the *P. (?) major* lineage is continued into the late Uintan of North America, when it is represented by "*Mimocyon*" *longipes*. We do, however, include the Chinese species, *Miacis lushiensis* Chow, 1975, in the genus *Miacis*.

ing shelf; anterior and posterior ridges from the apex of the main cusp are straight and slope directly downward to the accessory cusp, and are not constricted in any way; P^3 protocone absent; lingual and buccal margins of P_4 irregular in outline; M_2 trigonid cusps well-developed, trigonid relatively high.

DISCUSSION: The Aeluroida is a monophyletic clade that includes living carnivorans and former members of the primitive, early Tertiary "viverravine" carnivorans. The Aeluroida seem to be evolving a more hypercarnivorous morphology, such as that exhibited by many feloids. The hypothesis that all the taxa included within this group are more closely related to each other than to any other taxa indicates that it may be possible to more precisely determine the phyletic relationships of the early Tertiary Carnivora. Based on the distribution of derived characters within the Feliformia, it is possible to distinguish two clearly different and well-defined lineages, consisting of the totally extinct Didymictidae (Didymictida) as one branch, and the much more diverse fossil and living Aeluroida as the other. The morphology of the Aeluroida is extremely varied, but the derived characters presented in the diagnosis seem to ally all the diverse members of the infraorder. The taxa placed in the Aeluroida in this paper are: *Ictidopappus*, the Viverravidae (including only *Viverravus* and *Simpsonictis*), *Palaeogale* and the Feloidea (of Simpson, 1945 and most subsequent workers, but excluding the Nimravidae). However, the precise phyletic relationships of the controversial genera *Ictidopappus* and *Palaeogale* within the Aeluroida are uncertain, as is discussed thoroughly later in the systematic sections of this paper.

Conules are absent on both of the upper molars of the Aeluroida. All the taxa included within this group have simplified the structure of the trigon basin on M^1 and M^2 , as both the paraconule and metaconule are lost. This is an extremely derived condition in comparison to the large molar conules found in the Didymictidae, all primitive Carnivora and other mammalian outgroups. Large shear facets are well developed on the

paracone, metacone, and protocone of M^{1-2} , and the loss of the molar conules appears to be associated with the great emphasis on hypercarnivory and shearing in the molar trigons. The buccal ends of the preprotocrista and postprotocrista are weakly developed, indistinct, and low and do not add significantly to the topographic relief of the crown in the trigon basin.

The second posterior accessory cusp and notch on P_4 are not present in any Aeluroida, and their loss is assumed to be derived from the primitive condition of the presence of this cusp in the Feliformia. As discussed earlier, the presence of the second posterior accessory cusp is assumed to be primitive for the Carnivora and Feliformia, and reduction or loss of this cusp would be derived for any given taxon. *Didymictis* parallels the Aeluroida in the loss of this cusp. The simplification of the talonid of P_4 , and the loss of posterior accessory cusps occurs in many groups of Carnivora. This must have been derived independently in various lineages, based on its distribution in groups that are clearly not closely related, such as the Aeluroida, some Didymictidae and many Caniformia. However, because the Aeluroida can be assumed to be monophyletic on the basis of the most parsimonious distribution of derived characters found within the Carnivora, there is no reason to make the ad hoc assumption that the second posterior accessory cusp on P_4 is lost independently in the individual Aeluroida taxa. For this reason we consider the loss of the second posterior accessory cusp on P_4 to be a derived character uniting the Aeluroida.

A very distinctive character uniting the Aeluroida is the anteromedial position of the paraconid of M_1 , and the relatively distant separation of this cusp from the metaconid. The wide separation of the paraconid and metaconid results in an open-V on the trigonid, formed by the paralophid and protolophid. Primitively in feliforms, and carnivorans in general, the paraconid and metaconid of M_1 are closer together and form a much more closed-V on the trigonid. All Aeluroida have a much more open trigonid, and some groups within the Aeluroida (e.g.,

Palaeogale and the Felidae) may become even more derived in the opening of the trigonid-V by reduction of the metaconid and anteroposterior alignment of the paraconid and protoconid. Some advanced Caniformia parallel the Aeluroida through a similar opening of the trigonid of M_1 .

All Aeluroida reduce the cingulae on the upper and lower cheek teeth. The lingual and posterior talonid cingulae on P_4 are weak, as are the basal cingulae of the upper and lower molars. This contrasts with the primitive retention of well-developed cingulae in the Didymictidae (except *Protictis arophatos*).

The Aeluroida retain a suite of characters that are primitive for Carnivora and/or Feliformia, and are also found in the other major branch of the Feliformia, the Didymictidae. However, there are a number of primitive features that are maintained in the Aeluroida, but are modified by the Didymictidae. These characters (outlined in the diagnosis, above) serve to distinguish the Aeluroida from the Didymictidae, but only by enabling one to state that a taxon retaining these features is not a member of the Didymictidae.

ICTIDOPAPPUS SIMPSON, 1935

DISCUSSION: Simpson (1935) first described this very unusual, poorly known (represented by only one upper and one lower jaw) carnivoran. The animal's dentition was obviously well adapted for shear, as was discussed in detail by MacIntyre (1966). These two are the only workers that have considered the morphology and possible relationships of *Ictidopappus*. Simpson (1937) believed that *Ictidopappus* would be an ideal ancestor for *Viverravus*, except for the unusual proportions and simple structure of P_4 in the former genus. Simpson also hypothesized that P_4 in *Ictidopappus* could be structurally ancestral to that of *Viverravus*, although he saw no good evidence in support of this idea. MacIntyre (1966) criticized the notion that *Ictidopappus* might be ancestral to or closely related to *Viverravus* as he saw no special resemblance between the two genera. Any similarities between the two forms

were assumed to be parallelisms evolved for hypercarnivory.

Ictidopappus seems to share a number of derived features with the Feliformia and the Aeluroida, although the precise homologies of the characters are sometimes suspect. The genus is believed to have reduced the molar dentition to 2/2, as stated by Simpson (1935, 1937) and MacIntyre (1966). However, both the upper and lower jaws are broken immediately posterior to M_2^2 , and the presence or absence of M_3^3 cannot be determined with certainty. If the dental formula truly was M_{1-2}^{1-2} , this would correspond to the primitive dental formula found in all feliforms. The trigonid of M_2 is broken and represented only by an alveolus, but the talonid appears to be moderately elongate relative to the presumed size of the trigonid. The inferred ratio of M_2 talonid/trigonid length appears to be lower than that found in most feliforms, but higher than that found in the Caniformia. Also, the elongate oval outline of the talonid of M_2 is very similar to the feliform condition. There is a relatively large hypoconulid on M_2 in *Ictidopappus*, that is equal to, or greater than, the height of the hypoconid, as in other Feliformia. M^2 is reduced and is much smaller than M^1 , as in all feliforms that retain M^2 . In the Caniformia, M^2 is smaller than M^1 , but it is not as transversely narrow and anteroposteriorly shortened, as in the Feliformia.

P^4 in *Ictidopappus* is highly modified for shearing and is extremely worn and fractured on the only known maxilla. The parastyle is very large, high and an integral part of a long shearing ridge on P^4 . It is separated from the paracone only by a shallow concavity in the ridge and a narrow valley on the buccal portion of the tooth crown. The parastyle is higher and more robust than in most feliforms, but is similar in size (relative to the paracone) to the parastyle in some *Protictis*, Felidae, and Hyainidae. However, the incorporation of a large "parastyle" into a shearing ridge also occurs in some Nimravidae (here considered members of the Caniformia). The anterobuccal "cusp" in these nimravids is not considered homologous with the large parastyle of the Feliformia (see discus-

sion below). It is possible that a similar parallel development of a "parastyle" occurred in *Ictidopappus*, but the general morphology and topography of the cusp is similar to that in other feliforms. In the absence of evidence to falsify this homology, we reject the ad hoc assumption that this character is an adaptation for hypercarnivory evolved independently in *Ictidopappus*. Instead, we consider the enlarged parastyle a derived character for *Ictidopappus* and the Feliformia.

There is a lingual lobe on P⁴ for the protocone, although wear has removed all evidence of the cusp. The size of the lobe indicates that the protocone may have been a well-developed cusp, a primitive carnivoran character retained by the Feliformia, but the complete removal of this cusp by wear may alternatively signify that the cusp was smaller than in most feliforms. The protocone lobe of *Ictidopappus* is unusual for a carnivoran, in that it is relatively far posterior on the crown of P⁴. Within Carnivora the primitive protocone position is far anterior to the paracone, forming a distinct anterolingual projection on the tooth crown. The functional and phyletic significance of this character is unclear, but it may be an autapomorphy for *Ictidopappus*.

The structure of the carnassial notch of P⁴ is difficult to discern. There is a shallow, broad notch present in *Ictidopappus*, but there is a break in the tooth at, or slightly anterior to, the position of the deep, slitlike portion of the notch found in the Feliformia. If this break is in the position of the vertical, slitlike notch in feliforms, *Ictidopappus* may have had a similar notch. However, the available evidence indicates that there was not a deep, vertical notch in this genus, and the notch consisted only of a low concavity in the paracone-metastyle ridge. Both primitive feliforms and caniforms have at least some vertically oriented notching on P⁴, therefore, the notch on P⁴ in *Ictidopappus* may be very different from both of these conditions.

Ictidopappus resembles other Feliformia in the lack of a lingual cingulum continuous around the entire base of the protocone on the upper molars. This is a character that is

primitive for Carnivora, and therefore does not ally the various taxa that lack it. However, the Caniformia develop a continuous lingual cingulum, which excludes *Ictidopappus* from a position within that group.

P³ in *Ictidopappus* has a small lingual lobe for a protocone, although wear has obliterated any manifestation of this cusp. However, the position of this cusp is very different from the position of the protocone developed in *Protictis*. In *Ictidopappus* the lingual lobe is directly lingual, or posterolingual to the apex of the paracone, whereas the protocone in *Protictis* is located anterolingually on the crown of P³, far anterior to the apex of the paracone. The development of an internal expansion, and possibly a protocone cusp, on P³ appears to be different and independently derived in both *Ictidopappus* and *Protictis*.

Within the Feliformia, *Ictidopappus* appears more closely allied to the Aeluroidea than to the Didymictidae. The genus has an open-V on the trigonid of M₁ formed by a wide separation of the metaconid and the antero-centrally located paraconid. This condition is derived for all Aeluroidea and is not found in any of the Didymictidae. *Ictidopappus* also lacks conules on the upper molars, as in the Aeluroidea, but the large degree of wear on the molar crowns makes this assertion less certain, and subject to modification through the discovery of new material.

There are a number of characters in *Ictidopappus* that do not appear to be feliform, and others that are more similar to those of the Caniformia. As mentioned above, various P⁴ characters of *Ictidopappus* are difficult to discern and alternative interpretations to those given above are considered here. The protocone of P⁴ is located medial to the paracone and more posterolingually than in all other carnivorans, but is similar to the position in the Creodonta. The total lack of any trace of the protocone cusp on the well-worn crown indicates that the protocone may have been reduced in size, as is found in the Caniformia. The structure of the carnassial notch in P⁴ is equivocal, and is equally dissimilar to the notch in both feliforms and caniforms. Homology of the "parastyle"

of P_4 is uncertain; although we consider it a true, enlarged, feliform, cingular parastyle cusp, it is possible that *Ictidopappus* paralleled some nimravids in the partial elaboration of the anterior ridge of the paracone into a parastyle-like crest on a shearing blade (see fig. 9).

The relative size of the talonid and trigonid of M_2 is uncertain, but the moderate elongation of the talonid may be intermediate between the conditions exhibited by the Feliformia and Caniformia. *Ictidopappus* may, therefore, represent a caniform with a relatively long talonid.

Other workers have assumed that the molar formula of *Ictidopappus* was reduced to M_{1-2}^1 . However, the breaks at the posterior ends of both the mandible of the type (USNM 9296) and the referred maxilla (USNM 9295) do not preclude the possibility that M_3^1 were actually present in this specimen. If M_3^1 were retained, *Ictidopappus* would be excluded from the Feliformia, and would be more similar to the Caniformia in this primitive retention. Alternatively, *Ictidopappus* may be a very derived, early caniform that had already reduced the molar dentition to M_{1-2}^1 .

The morphology of the *Ictidopappus* P_4 is very distinctive, and very different from the morphology of P_4 in all other carnivorans. The anterior accessory cusp is small, weakly elaborated, high on the tooth crown, far anterolingual and connected to the main cusp by a strong, uninterrupted ridge. This differs greatly from the morphology in other feliforms, as well as other Carnivora. The Feliformia all have a small, but strong, anterior accessory cusp that is at the base of the trigonid of P_4 . The cusp in feliforms (and caniforms) appears to be an elaboration of an anterior, basal cingulum, and is separated from the main cusp by a distinct notch or wide valley. In contrast, the anterior accessory cusp in *Ictidopappus* is much higher on the trigonid, is much farther lingual, and is a swelling on the anterior end of a ridge from the main cusp, rather than a cingular cusp. There is a very slight lingual swelling of the enamel on the crown of P_4 , internal to the main cusp, that may represent a rudimentary

lingual accessory cusp. This is similar to the condition in *P. (Bryanictis) vanvaleni*, which has a definite lingual accessory cusp, and differs from all other Carnivora, which lack any indication of this cusp. Overall, the trigonid of P_4 in *Ictidopappus* appears much more molariform than the trigonid of any other carnivoran (except *P. (Bryanictis)*, which is only molariform in the development of a lingual accessory cusp); the anterior accessory cusp is high and far lingual (paraconid-like), rather than anterior, low and cingular; the lingual accessory cusp is rudimentary, but in the position of a lingual metaconid, rather than entirely absent; and the cusps are aligned in a trigonid-V, rather than anteroposteriorly in a straight line.

The talonid of P_4 is very short, wide, and weakly cuspidate. The talonid in *Ictidopappus* is largely formed by a strong, transverse, posterior cingulum and lacks significant basining. This differs greatly from the talonid structure in other Carnivora, in which the talonid is primitively longer, distinctly cuspidate, and well basined. Even in carnivorans that reduce the talonid of P_4 , there is generally greater cusp development, particularly on the high buccal ridge, and better basin development.

The outline of P_4 is short and triangular, rather than the elongate oval or elongate rectangular outline found in other primitive carnivorans. This suite of P_4 characters in *Ictidopappus* is unique among the Carnivora, and adds little information useful for determining the phyletic relationships of this genus, or any other carnivoran.

FAMILY VIVERRAVIDAE

WORTMAN AND MATTHEW, 1899

TYPE GENUS: *Viverravus* Marsh, 1872.

INCLUDED GENERA: *Viverravus* Marsh, 1872; *Simpsonictis* MacIntyre, 1962.

DISTRIBUTION: Middle Paleocene to ?late Eocene.

DIAGNOSIS: Members of the Aeluroidea and Feliformia that differ from all other members of these groups in the following derived features—the anterior accessory cusp on P_4 is far anterolingual and isolated from the main

body of the trigonid by a narrow constriction of the crown just posterior to the anterior accessory cusp; M_2 talonid extremely elongate due to enlargement of the hypoconulid and the posterior lobe of the talonid, hypoconulid large, expanded and bulbous with a distinct anterior facet for occlusion with the posterior margin of M_2 ; M_1 hypoconulid strong, posterocentrally located, and projecting posteriorly from the talonid margin; anterobuccal basal trigonid cingulum on M_1 weak; anterior trigonid notch on M_2 reduced, resulting in a continuous, low paralophid.

A number of primitive Aeluroida and Feliformia characters are retained by the Viverravidae that are modified by various other feliforms, including: small, low anterior accessory cusp on P_4 , separated from the main cusp by a broad, shallow concavity; narrow P_4 talonid, shallow talonid basin, and low lingual talonid ridge rimming the basin; molar trigonids high, particularly the trigonid of M_2 ; P^3 without a protocone; P_4 occlusal outline very irregular, not straight or arcuate; cingulae poorly developed; bulla unossified; postglenoid foramen large.

DISCUSSION: Following the erection of the Viverravidae by Wortman and Matthew (1899), usage of the family was abandoned by most workers. However, the concept of a closely allied group of genera was retained by Matthew (1909, 1915) and Simpson (1935, 1937, 1945) through use of a subfamily Viverravinae within the Miacidae.

We propose the resurrection of the family Viverravidae, although we restrict the Viverravidae to include only the genera *Viverravus* and *Simpsonictis*. We agree with Rigby (1980) that *Simpsonictis* is a valid, distinct, diagnosable genus. Furthermore, *Simpsonictis* is widely separated from the cluster of taxa allied in the genus *Protictis* and here grouped with *Didymictis* in the new family Didymictidae. We support MacIntyre's (1962) original recognition of the distinct nature of the material included in *Simpsonictis tenuis*, and because of the shared derived features between this genus and *Viverravus* (and the extremely close similarity of some aspects of the morphology between *Simpsonictis* and *V. acutus*) we ally these

two genera in a restricted concept of Wortman and Matthew's Viverravidae.

Simpsonictis tenuis is only known from a small cluster of lower dentitions collected from the San Juan Basin, New Mexico. Rigby (1980) named a new species of *Simpsonictis*, *S. jaynannei*, from the Paleocene Swain Quarry from northwestern Colorado. The known dental material does provide enough information to permit a number of important phyletic conclusions to be drawn. *Simpsonictis* is very similar in overall morphology to *Viverravus acutus*, particularly in P_4 and M_2 , which provided us with an indication that *Simpsonictis* might be closely allied to *Viverravus* rather than *Protictis*. Rigby (1980) mentions that personal communication from MacIntyre suggested that *Simpsonictis* might be related to *Viverravus*, although no explicit reasons for allying the two genera were given in that paper. The derived characters allying *Simpsonictis* with all other Aeluroida have been discussed previously, and the derived features that further unite the genus with *Viverravus* as a family within the Aeluroida are considered below.

The anterior accessory cusp on P_4 in the Viverravidae is located at the base of the trigonid and very far lingual of the main antero-posterior axis of the tooth. The cusp is small, as in primitive Feliformia, but its distinctly lingual position may be derived. There is a tight, narrow, transverse constriction of the tooth crown just posterior to the anterior accessory cusp on an anterior lobe of the crown of P_4 , which distinctly separates the anterior accessory cusp from the main cusp. There is a definite lingual inflection of this anterior lobe that coincides with the anterolingual positioning of the anterior accessory cusp.

The hypoconulid of M_1 in the Viverravidae is very well developed, high and located posterocentrally on the tooth crown. The hypoconulid also projects posteriorly from its position at the posterocentral margin of the talonid. This results in a distinct, but transversely narrow, tablike projection at the base of the talonid, that appears to articulate with the anterior edge of the trigonid of M_2 in a

lock-and-key type of arrangement. This unusual hypoconulid morphology is found in both *Viverravus* and *Simpsonictis*, but in no other Feliformia, nor in the Caniformia, and it appears to be a derived feature for the Viverravidae. However, in one outgroup taxon, *Leptonysson*, a similar projection of the hypoconulid occurs on both M_1 and M_2 . The lack of this feature in all the other outgroups examined, and its occurrence only on M_1 in the Viverravidae, would seem to indicate that it is a nonhomologous character evolved independently in both groups, rather than a primitive retention only in the Viverravidae (and no other Carnivora).

All Viverravidae have a very weak antero-buccal basal trigonid cingulum on M_{1-2} . The presence and strong development of this cingulum is primitive for all Carnivora, and is found in most of the Cretaceous outgroup taxa. In primitive Carnivora, the cingulum is present as a low, basal elaboration of the crown of M_{1-2} continuous along the anterior and buccal base of the trigonid. The Viverravidae reduce this cingulum to only a narrow, irregular, and sometimes discontinuous rim at the base of the molar trigonids. Some of the Didymictidae elaborate the antero-buccal basal trigonid cingulum into a low, wide shelf, whereas most other feliforms retain the primitive condition for this cingulum.

The anterior trigonid notch on M_2 is reduced in size in the Viverravidae, and the paraconid is relatively low. This results in a continuous, low, horizontal paralophid on M_2 and a reduction in the depth of the carnassiform notch. The primitive carnivoran condition of a high M_2 paraconid, a high paralophid with a deep vertical embrasure, and a deep, sharp carnassiform notch found primitively in the Didymictidae and other Feliformia is highly modified in the Viverravidae. Although the reduction of the paralophid is not as extreme in *Simpsonictis* as in *Viverravus*, it is greater than that observed in other Aeluroida, and it appears to be a derived feature uniting the two groups. Some species of *Didymictis* also reduce the paraconid of M_2 and paralophid, but this is in conjunction with a reduction of the size of

all the trigonid cusps and of the trigonid height as a modification of the M_2 trigonid as a flat grinding surface continuous with the talonid of M_1 .

The Viverravidae differ strongly from the remainder of the Aeluroida in features of the basicranium. Based on the limited known cranial material for the Viverravidae (known only in *Viverravus*, see Matthew, 1909, as *Simpsonictis* is represented only by dental elements), the family lacked any indications of an ossified bulla and retained a large postglenoid foramen. The bulla in *Palaeogale* and the Feloidea is fully ossified, in contrast, and preserved basicrania are unknown for *Ictidopappus*. *Didymictis* also appears to lack an ossified bulla, based on an undescribed, well-preserved skull of *Didymictis* (AMNH 17030) from the Huerfano (see below). As mentioned above (see Systematics—Carnivora), an unossified bulla is probably primitive for the Carnivora, but the hazards of basing such a statement on the limited material available for early, primitive members of the group are obvious. The absence of an entotympanic bulla, or any indications of its presence in the surrounding bones of the basicranium, indicates that the ear region in the Viverravidae remained more primitive than those of the closely related *Palaeogale* and the Feloidea.

Viverravus also retains the large postglenoid foramen primitively found in the Carnivora. The foramen is situated far postero-externally on the postglenoid process, at the posterior margin of the ventral contribution of the squamosal to the postglenoid region (see fig. 7), and widely separated from the posterior wall of the glenoid fossa. In the Caniformia, and other Mammalia, the postglenoid foramen is also large, but it is located far anteromedially on the postglenoid process, directly posterior to the glenoid fossa, and high on the posterior wall of the fossa. Even in Caniformia with a long basicranium, similar in length to that of *Viverravus*, the foramen is far anterior and just lateral to the location of the fissura glaseri. Therefore, the posteroexternal position of the postglenoid foramen does not appear to be directly correlated with basicranial length. The po-

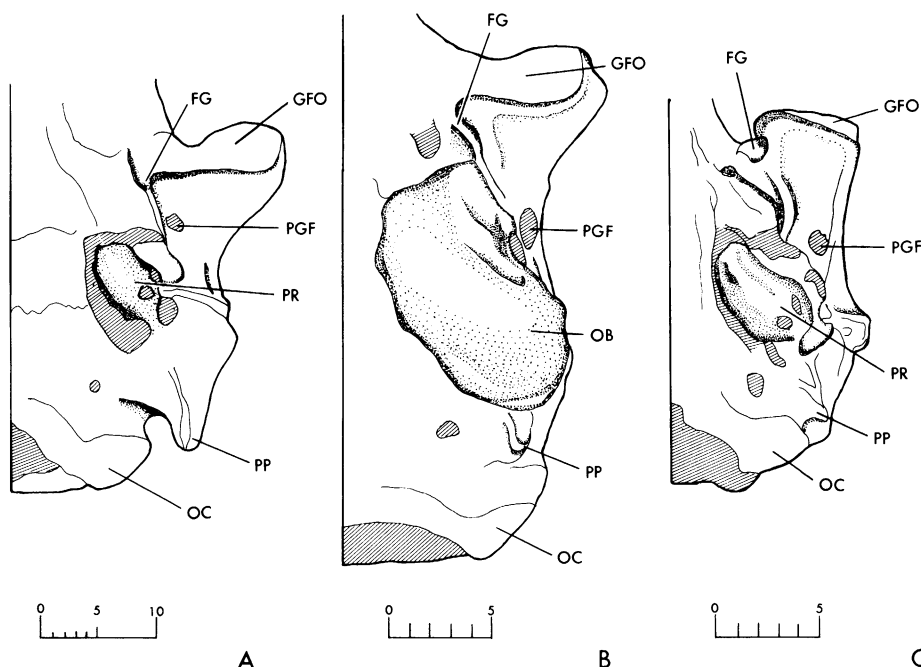


FIG. 7. Comparative basicrania of A) *Vulpavus* (AMNH 12626), B) *Palaeogale* (AMNH 25449), and C) *Viverravus* (AMNH 12621). Views of left, ventral surfaces of the basicrania; illustrations partially restored based on right side of skull, when specimen is damaged. Scales in millimeters. FG—fissura glaseri; GFO—glenoid fossa; OB—ossified bulla; OC—occipital condyle; PGF—postglenoid foramen; PP—paroccipital process; PR—promontorium. Hatching indicates foramina or areas covered by matrix.

sition of the postglenoid foramen in *Viverravus* appears to be very different from, and much more derived than, the primitive position for the Carnivora. In the Feloidae, the postglenoid foramen is extremely reduced in size, or absent. When present in feloids, this foramen is located somewhat anteromedially. It is unclear whether the foramen even passes any significant circulatory vessel, or whether it just serves as a nutrient foramen in those feloids that do retain it. *Palaeogale* has a large postglenoid foramen in a position very similar to that found in *Viverravus*. *Didymictis* (based on AMNH 17030) has a large postglenoid foramen that is located far anteromedially, just posterior and external to the fissura glaseri. The posteroexternal location of the postglenoid foramen is certainly derived over the primitive position for the Carnivora, and it probably represents a synapomorphy for the Viverravidae and *Palaeo-*

gale (see also the section on *Palaeogale*, below).

We agree with MacIntyre's (1966) criticism of Simpson's (1937) idea that *Ictidopappus* might be ancestral to *Viverravus*, as *Ictidopappus* is certainly a very unusual and derived form. However, as discussed in the section on *Ictidopappus*, we do consider this genus to be related to *Viverravus* and *Simpsonictis* (the Viverravidae), for both of these taxa are members of the Aeluroida and are phylogenetically distant from the other early Tertiary Feliformia. The characters distinguishing *Ictidopappus* from the Viverravidae were already considered in the systematic discussion of that genus, and in the earlier parts of this discussion detailing the derived features uniting the Viverravidae. *Ictidopappus* is here excluded from the Viverravidae, but included within the Aeluroida, because it lacks the derived features allying *Viver-*

ravus and *Simpsonictis* and it has the derived characters of the infraorder. *Ictidopappus* is not more closely related to *Viverravus* and *Simpsonictis* than to any other members of the Aeluroida.

Viverravus has a number of important features that are more advanced than those found in *Simpsonictis*. P_3 is higher than P_4 ; metaconid height is lower than the paraconid on M_1 , and the metaconid is directly lateral to the protoconid; the cristid obliqua on M_{1-2} is aligned more directly anteroposteriorly, and the sulcus obliquus becomes more transversely narrow; and some species develop a distinct hypocone as an elaboration of the postcingulum.

The enlargement of P_3 to a greater overall size than P_4 , in *Viverravus*, is unusual and derived for the Carnivora. All other early Tertiary Caniformia and Feliformia, except *Procynodictis* and *Daphoenictis*, have P_3 much shorter in length and lower in height than P_4 . In *Viverravus*, P_3 increases in length (although it generally remains shorter than P_4), and the height of the main cusp on P_3 is always greater than on P_4 .

The metaconid of M_1 is reduced in all *Viverravus*, and the paraconid is relatively enlarged, particularly in more derived species. The combination of the open-V on the trigonid of M_1 in all Aeluroida, enlargement of the paraconid, and reduction of the metaconid results in an enlarged and elaborated, more anteroposteriorly aligned, lower carnassial blade. Shear on the paralophid and the carnassial notch of M_1 is thereby further emphasized, and shear on the posterior face of the trigonid characteristic of the Didymictidae is reduced. The metaconid is farther anterior on the trigonid, and is located directly lateral to the protoconid, rather than posterolingual to it, as in other Carnivora. Any posterior shear occurring on the trigonid of M_1 is therefore oriented more transversely, rather than obliquely.

In all *Viverravus* the cristid obliqua on M_{1-2} is aligned parallel to the anteroposterior axis of the tooth, rather than following the primitive oblique course across the talonid. The sulcus obliquus is transversely narrow and deep, presumably as a result of

the anteroposterior alignment of the cristid along the buccal margin of the tooth. The talonid becomes trenchant in *Viverravus*, due to the emphasis on the large, anteroposterior ridge formed by the cristid obliqua.

Some species of *Viverravus* parallel advanced Caniformia in the development of a distinct hypocone cusp. This cusp is an elaboration of the well-developed posterolingual cingulum present at the base of the protocone in all *Viverravus*.

In many ways *Simpsonictis* remains primitive with respect to *Viverravus*. *Simpsonictis* lacks all the derived features mentioned above for *Viverravus*, but there are a number of advanced features that characterize the genus. Two of the most distinctive characters of the lower dentition of *Simpsonictis* are the moderately large anterior accessory cusp on P_4 and the development of high, sharp, piercing cusps on all the cheek teeth. The development of an enlarged P_4 anterior accessory cusp may be derived for *Simpsonictis*, and in some ways it parallels the enlargement of this cusp in *Protictis*. However, the cusp in *Simpsonictis* is never so high or large as in *Protictis*, nor is it elaborated into an anteroposteriorly aligned, laterally compressed, robust blade as in *Protictis*. Furthermore, P_4 lacks the deep notch between the anterior accessory cusp and the main cusp found in all the Didymictidae. For these reasons, and because of the many derived features supporting the phyletic separation of *Simpsonictis* and *Protictis*, it is assumed that the moderately large P_4 anterior accessory cusp in *Simpsonictis* is a feature uniquely derived within the Aeluroida.

Simpsonictis is also the only member of the Feliformia to modify its dentition for piercing (and presumably insectivorous hypercarnivory). All the cusps are high, thin, sharp and conical, rather than the more robust and shorter cusps found primitively in the Feliformia. MacIntyre (1962, 1966) provided a detailed discussion of this aspect of the dentition of *Simpsonictis*, and it is sufficient to point out here that this modification of the cusp morphology is very derived for the Carnivora, is unique to *Simpsonictis*,

and it serves to distinctly define *Simpsonictis* as a monophyletic taxon.

PALAEOGALE VON MEYER, 1846

DISCUSSION: Simpson (1946) provided the most recent review of the morphology and relationships of *Palaeogale* in his discussion on *Palaeogale*, *Plesiogale* and *Plesictis*. In this study Simpson synonymized the American genus *Bunaelurus* with *Palaeogale*. Previous workers had used the presence of M^2 in *Bunaelurus* to distinguish this genus from *Palaeogale*, which lacks M^2 . Simpson did not consider this single character difference to be generically significant, and he included a lengthy discussion of his reasons for concluding that the presence or absence of M^2 was insufficient grounds for separating these two genera (see also the discussion in this paper, sections on *Plesiomiaceis* and *Quercygale*). *Palaeogale*, *Plesiogale*, and *Plesictis* were all believed to be "the earliest definitely recognizable mustelids . . ." (Simpson, 1946, p. 1), based on the dentition and cranial foramina of these forms. In his redefinition of *Palaeogale* and *Plesiogale*, Simpson (1946, pp. 12–13) pointed out a number of features that distinguish the two genera, and that also support the assignment of *Palaeogale* to the Feliformia rather than the mustelid Caniformia.

Hunt (1974b) briefly mentioned *Palaeogale*, which he believed was very similar to *Viverravus*. There was no discussion of the basis for allying *Palaeogale* with *Viverravus*, other than the suggestion that the two exhibited many morphological similarities.

The precise phyletic position of *Palaeogale* is debatable. It appears that much of the reason Simpson considered it a mustelid was its supposed close alliance with *Plesiogale* and *Plesictis*, which may well be early members of the Mustelidae. However, Simpson did not provide any clear documentation or solid evidence for his assignment of *Palaeogale* to the Mustelidae, and we believe that many of the characters presented in his diagnosis, as well as others considered during this investigation, support an alternative placement of the genus in the Feliformia.

Palaeogale has a number of features that appear to be derived in common with all other Feliformia. A moderately large parastyle cusp on P^4 is present in *Palaeogale*, although its size is variable in different species of the genus. The size of the parastyle varies from small to moderately enlarged, but in all cases the parastyle is an elaboration of the anterior basal cingulum on P^4 and is not a modification of the anterior paracone ridge, as in the Nimravidae. Those species of *Palaeogale* that have a large parastyle do enlarge the cusp to a similar degree to that found in all other Feliformia.

As pointed out by Simpson (1946, p. 12), there is a narrow, deep cleft on P^4 separating the paracone portion from the metastylar part of the elongate blade. This is the same as the derived condition of the metastyle notch in the Feliformia, and is not similar to the notch exhibited by the Caniformia. Furthermore, all the living Mustelidae lose the carnassial notch on P^4 , altogether, and only a broad, shallow concavity on the metastylar blade remains in these forms.

All *Palaeogale* lack M_3 and M^2 is reduced in size, or is absent. Both of these are derived morphologies that are found in the Feliformia. However, advanced caniforms (such as the Mustelidae) also lose M_3 , and strongly reduce, or lose, M^2 . Depending on the determination of the phyletic affinities of *Palaeogale* based on the distribution of other derived characters, as well as this one, one could consider the genus a member of either the Feliformia or of a derived branch of the Caniformia. The lack of many derived mustelid characters in *Palaeogale*, as well as the presence of derived feliform features, lead us to hypothesize a phyletic position within the Feliformia for this genus. *Palaeogale* would be more advanced than most of the primitive feliforms, as it has reduced M^2 to a minute size, or even lost it altogether, in contrast to the larger and more functionally important M^2 of early feliforms.

The lower dentition of *Palaeogale* has a number of features that place the genus within the Feliformia, in general, and specifically within the Aeluroida. M_2 is very reduced in

overall size, but the tooth remains functional and has an elongate oval outline, rather than the short squared or rectangular outline characteristic of the Caniformia. It is difficult to discern the standard molar cusp pattern on M_2 of *Palaeogale*, but the length of the talonid portion does seem to be equal to or greater than the length of the trigonid. This would be a derived feature common to both *Palaeogale* and the other Feliformia. M_2 s of the other "mustelids" discussed by Simpson, *Plesiogale* and *Plesictis*, are not described as having the derived, feliform, elongate oval outline mentioned for *Palaeogale*.

Palaeogale also has the open trigonid-V on M_1 characteristic of all the Aeluroida. The paraconid is relatively large, far anterior on the trigonid, and located more buccally (closer to the midline) than the paraconid in primitive feliforms and Carnivora. The carnassial notch between the paraconid and protoconid is deep and the paralophid is well developed and aligned more anteroposteriorly than in some feliforms (e.g., the Didymictidae). Anterobuccal shear on the paralophid is greatly emphasized and posterior shear on the protoconid is very reduced, as in all Aeluroida. This results in an open-V and anteroposteriorly oriented paralophid on the trigonid of M_1 . *Palaeogale* further modifies the trigonid of M_1 by losing the metaconid entirely. Many other Aeluroida (particularly within the Felioidea) reduce the metaconid of M_1 but none have totally eliminated the metaconid as a distinct cusp. Some advanced Nimravidae also lose the metaconid of M_1 , but since this only occurs in the more derived members of the family, it may be hypothesized that the loss of the metaconid occurred independently in *Palaeogale* and only some nimravids.

The upper molars in *Palaeogale* are more similar to feliforms than caniforms in their lack of a continuous lingual cingulum around the base of the protocone. Even though the upper molars of *Palaeogale* are reduced in size, particularly in the lingual portion of the teeth, there is no indication of any development of a single, strong lingual cingulum that entirely encircles the protocone. In contrast, *Plesiogale* and *Plesictis* do seem to have the

elaborate, continuous lingual cingulum that is derived for the Caniformia. This lack of a lingual cingulum does not necessarily ally *Palaeogale* with the Feliformia, as it is only a retention of a primitive character, but it does indicate that *Palaeogale* may not occupy a position within the Caniformia, as here defined. The Nimravidae also lack the modified cingulum, and it is conceivable that *Palaeogale* may be allied to this family (based on other characters, see below).

The protocone of P^4 in *Palaeogale* is relatively small and is closer in relative size to the reduced protocone of caniforms than to that of feliforms.

If *Palaeogale* is a member of the Feliformia, the precise phyletic position of the genus must then be determined. *Palaeogale* does not have any of the derived features that are diagnostic for the Didymictidae, but it does possess the characters that are derived for the Aeluroida. The open-V trigonid on M_1 is present, as discussed above, and the absence of conules on the upper molars is also characteristic of *Palaeogale*. Is *Palaeogale*, then, more closely related to *Viverravus*, as suggested by Hunt (1974b), or to the Felioidea, within the Aeluroida?

Although Hunt (1974b, p. 1039) stated that the ancestry of *Palaeogale* could be traced directly to the closely related *Viverravus minutus*, he gave no direct evidence for this and provided only a brief discussion of his reasons for allying the taxa. Hunt refers to the similarities in the basicranial structure and a "complex of cranial features" (1974b, p. 1039), but the reader may only indirectly infer the precise nature of these characters.

Palaeogale and *Viverravus* have a large postglenoid foramen that is located far posteroexternally on the postglenoid process of the squamosal. The large size of the foramen is primitive for all Eutheria, but the position of the foramen is certainly derived within the Carnivora. It seems likely, then, that the posteroexternal position of the postglenoid foramen is a derived feature uniting *Palaeogale* with the Viverravidae. This would agree with the relationship between the two genera proposed by Hunt. As no other Carnivora,

or Eutheria that we have observed, exhibit this derived morphology of the postglenoid foramen we feel that this character unites *Palaeogale* and the Viverravidae.

Palaeogale and *Viverravus* share the derived basicranial morphology of extreme reduction of the paroccipital and supraoccipital processes (see fig. 7). Other Carnivora (e.g., Feloidae, *Vulpavus*, other Caniformia, etc.) have these processes moderately well developed, as do the Creodonta and members of other eutherian outgroup taxa (see van der Klaauw, 1931, pp. 95–96 for a detailed discussion of the paroccipital morphology in the Creodonta and the primitive Carnivora). According to Matthew (1910b; as cited in van der Klaauw, 1931, p. 95): “the paroccipital process is short and backwardly directed, . . . a primitive eutherian character common to nearly all Eocene mammals.” The great reduction in size of these processes, and the resultant similarities in the morphology of these areas of the basicranium are derived features that would closely relate *Viverravus* and *Palaeogale*, to the exclusion of any other Carnivora for which basicrania are known.

Hunt may also be referring to basicranial length and overall similarity of the basicranium of the two genera in his suggestion of their close relationship. The basicrania of *Palaeogale* and *Viverravus* are generally similar, but most of these features are primitive retentions in both. Without an explicit analysis and discussion of the polarity of the supposed basicranial features allying the two genera, it is impossible to evaluate their utility in determining the precise phyletic relationship of *Palaeogale* and *Viverravus*. Such an analysis is not undertaken in this project.

An alternative hypothesis of relationship for *Palaeogale* within the Aeluroidea would be a close alliance with the Feloidae. *Palaeogale* may share the derived development of an ossified, bipartite bulla with the feloids. The bulla is known to be totally ossified in *Palaeogale*, although there is no ontogenetic evidence as to the percentage of the bulla contributed by either the ecto- or ento-tympanic components. All feloids also possess a completely ossified bulla, whereas the only

other known member of the Aeluroidea with a well-preserved basicranium, *Viverravus*, lacks any indication of an ossified bulla. If the lack of an ossified bulla is primitive for the Carnivora and the Feliformia, the presence of an ossified bulla in *Palaeogale* and the Feloidae would indicate a closer phylogenetic relationship between these taxa than between *Palaeogale* and any other Aeluroidea. However, *Palaeogale* lacks the ectotympanic septum in the bulla found in all members of the Feloidae. This indicates that the two groups might share only the ossification of the bulla, and *Palaeogale* remains more primitive in the lack of any development of the ectotympanic into an internal septum in the bulla.

The large size of the postglenoid foramen also excludes *Palaeogale* from a position within the Feloidae, but it does not preclude a closest sister group relationship between *Palaeogale* and the Feloidae.

The only other reasonable alternative hypothesis of relationship for *Palaeogale*, would be a close affinity with the Nimravidae. *Palaeogale* has the reduced upper and lower dental formulae characteristic of the nimravids. The Nimravidae reduce the molar dentition to M_{1-2}^1 , however, *Palaeogale* variably reduces it to $M_{1-2}^{1 \text{ or } 2}$.

The bulla is totally ossified in *Palaeogale* and some Nimravidae. However, total ossification of the bulla in the Nimravidae is only known for certain in the advanced nimravid *Barbourofelis*. Most nimravids, such as *Di-nictis* and *Nimravus*, never preserve a totally ossified bulla; the bulla is always broken and fragmented ventrally. Hunt (1974b) believed that this was just an artifact of preservation, and that all nimravids would have had a completely ossified bulla, in life. However, it is just as reasonable to assume that the bulla was only partially ossified in the primitive Nimravidae, and that the preservation observed in the large collections of these forms is indicative of the true condition of bullar ossification in the living animals. Both the Nimravidae and *Palaeogale* retain the primitive condition of a lack of any true septum within the bulla.

Palaeogale and the Nimravidae share a

similar M¹ morphology, but some of these features are also shared by the feliforms, *Ictidopappus* and the Feloidea, and may just be convergent adaptations to hypercarnivory. The general tooth outline is similar, in that there is a large parastyle wing, very small metastylar wing, robust buccal margin, anteroposteriorly shortened lingual margin, and transverse elongation of M¹. The protocone is the only internal cusp, and the lingual cingulum is extremely weak, or absent, and is not continuous around the base of the protocone. The size of M¹ is also very small, in comparison to P⁴ size and the size of M¹ in primitive Carnivora. The lack of continuity of the cingulum around the base of the protocone is a primitive retention and cannot be considered as indicative of special relationship between *Palaeogale* and the Nimravidae. Reduction in the size and the similarity in shape, of M¹ may be derived for these two taxa, but similar reduction and morphology also occurs in some Feliformia.

The metaconid of M₁ is absent in *Palaeogale* and in some Nimravidae, whereas other nimravids retain a small M₁ metaconid. In this case, either *Palaeogale* is more closely related to some advanced nimravids, than all the nimravids are to each other, or the loss of the metaconid on M₁ occurred independently in both groups. If the latter is the case, then the loss of the metaconid in *Palaeogale* and some Nimravidae cannot be considered a derived character between the two taxa.

All Nimravidae lack a true, basal cingulum parastyle on P⁴, whereas at least some species of *Palaeogale* exhibit a large parastyle. If *Palaeogale* is considered a close relative of the Nimravidae, within the Caniformia, then the species with a relatively large parastyle must be among the most primitive Caniformia, as they would have retained the primitive eutherian condition of a moderately well-developed P⁴ parastyle. The more advanced "species" of *Palaeogale* that reduce the parastyle would then be more closely related to the Nimravidae, which lose the cusp entirely, and the genus *Palaeogale* would be paraphyletic. Furthermore, the reduction and loss of the parastyle of P⁴ would have to be independently derived in both the Nim-

ravidae and the remainder of the Caniformia, as the earliest nimravid, *Palaeogale*, would retain a relatively large parastyle.

The Nimravidae also lack the derived, slit-like, P⁴ metastyle notch found in *Palaeogale* and the Feliformia, and their postglenoid foramen remains in the primitive anteromedial position on the postglenoid process, and is not located far posteroexternally as in *Palaeogale* and *Viverravus*.

The primitive lack of a teres process of the scapula in *Palaeogale* excludes this genus from a close phyletic relationship to the Nimravidae and other Caniformia (see below).

It seems most parsimonious, at this time, to include *Palaeogale* within the Feliformia, as the closest sister group to the Viverravidae. We prefer to group *Palaeogale* and the Viverravidae in the superfamily Viverravoidea Wortman and Matthew, 1899.⁸ However, the character contradictions and uncertainties discussed above, indicate that this is an equivocal hypothesis of relationship readily subject to modification based on rigorous testing of the hypothesis and more detailed analyses of character distributions between the taxa considered above.

SUPERFAMILY FELOIDEA HAY, 1930

INCLUDED TAXA: Hyaenidae, Felidae, and Viverridae.

DISTRIBUTION: Late Eocene to Recent.

DIAGNOSIS: Aeluroidea that differ from all other members of the Aeluroidea in the development of the following derived features—ossified, bipartite bulla with a large ectotympanic septum; great reduction or loss

⁸ Article 36 of the International Code of Zoological Nomenclature states that a name proposed for a taxon in any category in the family-group (tribe, subfamily, family, superfamily) has priority in the naming of any other category in the family-group. Therefore, the erection of a family Viverravidae by Wortman and Matthew in 1899 established nomenclatural priority for all other taxonomic ranks in this family-group. Our use of the superfamily Viverravoidea is simply recognition of the existence of a taxon implicit in the prior naming of the family Viverravidae.

of the postglenoid foramen (i.e., effective loss of venous drainage of the cranium via this foramen in all Feloidea); scaphoid and lunar united into a single ossification, the scapho-lunar; paroccipital process broadly based and closely appressed to the posterior wall of the bulla; development of an intracranial arterial rete in the orbital region, internal carotid artery reduced in size, or vestigial.

DISCUSSION: The Feloidea is a monophyletic taxon that includes all the living and fossil members of the families Hyaenidae, Viverridae, and Felidae, of Simpson (1945) but excludes the Nimravidae as used in this paper. An alliance of the felids, hyaenids, and viverrids results in a grouping of taxa with a varied suite of dental, skeletal, and soft anatomical modifications. Such an assemblage of taxa that have evolved numerous autapomorphies in the various familial lineages represents only the most basic hypothesis of relationships for these groups. The characters used in the diagnosis above distinguish the Feloidea from all other Aeluroidea and Feliformia, and indicate the close phyletic relationship of the three included families. We do not, however, attempt to resolve this trichotomy in any further detail, as we recognize that the relationships of the diversity of taxa included within the Feloidea must be considered with much closer scrutiny than is possible, or desirable, in this paper. Various aspects of the phylogeny of the three living feliform families are currently under study by numerous other workers.

An important feature uniting all the Feloidea is the development of a complete, large, ectotympanic septum within a totally ossified, bipartite (ectotympanic and entotympanic) bulla. All Feloidea share the derived condition of a large entotympanic (especially the caudal entotympanic) component, and a smaller ectotympanic component forming the bulla. The composition and morphology of the septum varies within the Feloidea, but all the members of the superfamily have a large, primary ectotympanic component of the septum. Hunt (1974a) showed that both felids and viverrids (except *Nandinia*) have a true, bilaminar septum bullae formed by

the inflected edges of the ectotympanic and the caudal entotympanic. Hyaenids appear to have a septum with only a tympanic contribution, and would therefore lack a true septum bullae, according to Hunt. Nonetheless, all feloids have a complete, large ectotympanic septum that divides the bulla into two separate chambers. This contrasts strongly with the internal construction of the bulla in both *Palaeogale* and all Caniformia with an ossified bulla. *Palaeogale* has a completely ossified bulla (although without early ontogenetic material, the relative proportions of the ecto- and ento-tympanic contributions are indeterminable), but lacks any indication of the development of an internal septum, either ectotympanic or entotympanic. Within the Caniformia, members of the Canidae develop a small caudal entotympanic septum, but it is in a different topographic position than in the Feloidea, it is never so large as in the Feloidea, nor is there any ectotympanic component to the septum such as that found in all the Feloidea.

The postglenoid foramen is extremely reduced in size, or absent, in all Feloidea. Those feloids that do retain a small foramen on the postglenoid process may have it variably developed on either side of the skull of a single individual. However, when the foramen is present, it is positioned far anteromedially on the basicranium. This is similar to the location of the large postglenoid foramen of the Caniformia, Creodonta and other eutherians, but differs from the extreme posteroexternal position found in the long-skulled *Viverravus*, and the slightly more moderate posteroexternal position exhibited by *Palaeogale*, with a shorter basicranium (see previous section).

It appears, therefore, that the loss of venous drainage of the head through the postglenoid foramen is a derived feature that unites the Feloidea. Venous drainage of the cranium and inferior petrosal sinus would be captured by another vessel, and at that point there would not be a significant vein or venous circulation passing through the postglenoid foramen. This would result in a great reduction of the size or total loss, of the postglenoid foramen. All other Carnivora, except

some aquatic carnivorans and some Nimravidae, retain the large, primitive postglenoid foramen and the passage of significant venous circulation.

The Feloidae are derived in the development of a single scapholunar ossification. Fusion of the independent scaphoid and lunar bones occurs a number of times in the Eutheria, but it may be hypothesized to have occurred only once in the phylogenetic history of the Feliformia. All the primitive feliforms for which feet are known have independent ossification of the scaphoid and lunar, as do many of the primitive caniforms. This feature was used by most of the early workers to ally all the primitive Carnivora in the Miacidae. A separate scaphoid and lunar may therefore be assumed to be the primitive condition for Carnivora. More advanced Caniformia also evolve a single scapholunar bone, but probably independently from the Feloidae, as the more primitive members of both suborders have a separate scaphoid and lunar. The hypothesis that a scapholunar was evolved twice within the Carnivora, rather than only once, is based on parsimony arguments; fewer assumptions of parallel evolution of derived features are required if the "miacids" are included in the Caniformia and Feliformia, than if the later Tertiary carnivorans are considered a monophyletic group from which most "miacids" are excluded (see fig. 8).

All Feloidae have a laterally expanded, broadly based paroccipital process that is very closely appressed to the posterior wall of the bulla. The process is curved and cup-shaped and forms a cradle that extends anteriorly along the posterior and ventral walls of the bulla (see Van der Klaauw, 1931, pp. 100–101). This cupping of the bulla by the paroccipital and enlargement of the process, is derived over the condition found in out-group taxa such as the Creodonta, Caniformia, and *Palaeogale*, and it appears to be a good synapomorphy for the Feloidae.

Davis and Story (1943) and Hunt (1974a) provided description and discussion of the internal carotid circulation in Carnivora. Evidence from these studies indicates that all Feloidae are derived in that they develop

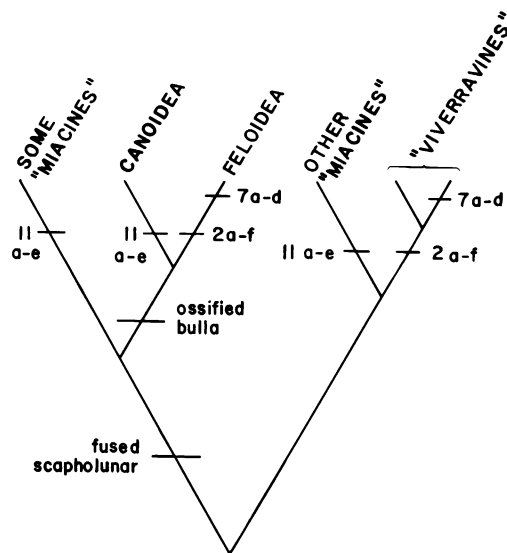


FIG. 8. Hypothesis of monophyly for the "Fissipeda." Traditional phylogeny in which the Feloidae and Canoidea (of Simpson) are most closely related to each other, to the exclusion of the "Miacoidae," based on the derived characters "ossified bulla" and "fused scapholunar bone." The numbers and letters are character contradictions and refer to the derived features summarized in the Phylogeny of the Carnivora section. Compare this phylogeny to the more parsimonious, alternative arrangement proposed in figure 4 and the Phylogeny of the Carnivora section. Some "miacines" refers to those "miacines" that have a fused scapholunar—*Vassacyon*, *Procynodictis*, and some *Vulpavus*; other "miacines" are those that have independent scaphoid and lunar bones.

an intracranial arterial (anastomatic branch of the external carotid) rete in the orbital region, and may reduce, or even lose entirely, the median internal carotid artery. The median internal carotid artery is absent in all Hyaenidae; greatly reduced, or vestigial, in the Felidae; greatly reduced or absent in *Nandinia*, and less reduced in all other Viverridae (Hunt, 1974a, p. 47).

A combination of the primitive Aeluroidea features and the derived characters for the Aeluroidea and the Feloidae may be assumed to represent the primitive morphotype (for the features considered here) for all the Feloidae. All the families within the Feloidae

have evolved divergent and characteristic specializations.

SUBORDER CANIFORMIA KRETZOI, 1943

INCLUDED TAXA: *Uintacyon*, *Miacis*, *Palaeoarctonyx*, *Tapocyon*, *Vulpavus*, *Vassacyon*, *Oödetes*, *Quercygale*, *Procyonodictis* (including "*Plesiomiacis*"), *Nimravidae*, and all other taxa included in Tedford's (1976) Caniformia.

DISTRIBUTION: Early Eocene to Recent.

DIAGNOSIS: Carnivorans that differ from all other Carnivora in the development of the following derived features—loss of the calcaneal fibular facet in the pes; great reduction or absence of the parastyle on P^4 ; reduction in size of the protocone of P^4 ; lingual cingulum on all upper molars complete around the base of the protocone; large teres major process on the scapula (in the taxa for which this region of the scapula is preserved).

Members of the Caniformia primitively retain the following carnivoran characteristics: metastyle blade of P^4 elongate with a broad, shallow carnassial notch; M_2 talonid shorter than the trigonid; M_1^{1-3} present, M^2 large and well developed; hypoconid on M_{1-3} robust, forming the largest talonid cusp; M_{1-2} talonid basins moderately wide; M_{1-2} trigonids high, paraconid < metaconid < protoconid size, trigonid cusps form a relatively closed-V; P_4 anterior accessory cusp small and separated from the main cusp by a broad valley; P_4 talonid long and with two posterior accessory cusps; conules present on all upper molars; independent ossification of the scaphoid, lunar, and centrale; bulla unossified.

DISCUSSION: The Caniformia represent the subordinal division of the Carnivora complementary to the Feliformia. As originally constructed by Kretzoi (1943, 1945) the Caniformia included all the members of Flower's Arctoidea and Cynoidea, the Miacidae of Matthew, and the aeluroid Hyaenidae and Viverridae. Tedford (1976) restricted usage of the Caniformia to the Canoidea and Pinipedia of Simpson (1945). We follow Tedford's usage, but we also include the "miacine miacids" within the Caniformia. Further,

a number of taxa that have previously been considered members of the Felioidea or Viverravidae appear to be members of the Caniformia, as is discussed later.

The inclusion of the early Tertiary "miacines" within the Caniformia results in a bipartite division of the Carnivora into two monophyletic taxa that include all the known early Tertiary, late Tertiary, and living carnivorans. Such an arrangement provides a vertical hypothesis of relationship for all the Carnivora and may serve to bridge the phylogenetic gap between the archaic and the modern carnivoran families lamented by Tedford (1976, p. 364). This paper, however, does not attempt to determine the phyletic relationships of the "miacines" in any more detail than to assign them to the Caniformia. Determination of the precise relationships of the various "miacine" genera would be an important and useful study and would provide insight into the early evolution of the caniform Carnivora.

Matthew (1909) pointed out that the "miacine miacids" differed from the "viverravines" in the loss of the calcaneal fibular facet in the pes. This character is a derived feature uniting the "miacines" and all the rest of the Caniformia. Matthew's statements about the "miacine" foot were based largely on articulated skeletal material assignable to *Vulpavus*, as postcranial elements definitely attributable to other "miacine" genera were unknown. However, based on information from the *Vulpavus* specimen illustrated by Matthew (1909, AMNH 12626, type of *Vulpavus profectus*), and on specimens assigned to *Miacis*, *Uintacyon*, and *Hesperocyon*, primitive caniforms had already lost the calcaneal fibular facet primitively retained in the Feliformia, Creodonta, other eutherians, and the marsupials. A sampling of living Caniformia (*Taxidea*, *Ursus*, *Canis*, and *Mephitis*) indicates that these taxa, and presumably all the Caniformia, have lost an articular contact between the fibula and the calcaneum, and no longer retain a large dorsal facet on the calcaneum for articulation with the fibula. Some of the caniforms (e.g., some *Nimravidae*, *Mephitis*) even develop a lateral pro-

jection on the astragalus at the anteroexternal base of the astragalar fibular facet that acts as a mechanical stop to prevent the fibula from moving too far anterior, and that effectively eliminates any possibility of the fibula articulating ventrally with the calcaneum.

As early as 1899 (Wortman and Matthew, 1899) the degree of development of the parastyle of P^4 was used to distinguish two major groups within the early Tertiary Carnivora. All Caniformia greatly reduce or lose the cingular parastyle cusp on P^4 . Most of the caniforms lose the cusp and reduce the basal cingulum early in their phylogeny, and those that do retain the parastyle have reduced it to a very small swelling or cusplike on the anteroexternal portion of the basal cingulum. The presence of a small parastyle is primitive for the Eutheria, but extreme reduction of the cusp, and in some cases the supporting cingulum as well, is a derived feature uniting all the Caniformia.

The protocone of P^4 is reduced in size in all Caniformia. The primitive condition for all eutherians is a large, lingual protocone on P^4 , as is maintained by the Feliformia. Reduction of the protocone is less extreme in some of the early Tertiary caniforms than in later members of the suborder, but in all cases the cusp is lower in height and occupies a smaller area of the surface of the crown of P^4 than is primitively found in the Eutheria and Feliformia. Moderate reduction of the protocone in some primitive caniforms makes it difficult to distinguish between those taxa and members of the Feliformia with a relatively small protocone, on the basis of this feature alone. Nevertheless, the protocone is relatively reduced in all caniforms, and when analyzed in conjunction with other characters this derived feature may be used to unite the members of the Caniformia.

The Caniformia are derived in the development of a continuous lingual cingulum on the upper molars (Tedford, 1980, personal comm.). Primitive Carnivora have both a precingulum and a postcingulum at the base of the molar protocones, without a connection around the lingual base of the cusp. Can-

iforms elaborate on this condition and develop a lingual cingulum that completely encircles the base of the protocone, although in some Caniformia (e.g., *Oödictes*) the connection of the posterior and anterior cingulae is only very weakly developed. In contrast, the Feliformia retain the primitive separation and distinction of two cingular expansions on the lingual margin of the molar crowns. The morphology exhibited by the feliforms is also found in the outgroup taxa, which maintain separate postcingulae and precingulae. Most of the Caniformia develop a distinct hypocone cusp as an expansion of the posterior portion of the lingual cingulum, as do some Feliformia (e.g., some *Viverravus*). However, in the Feliformia the hypocone arises from an isolated postcingulum that is not continuous with the precingulum, and is therefore a feature derived independently from, and in a different manner than, the hypocone in the Caniformia. All caniforms develop the continuous lingual cingulum, whereas the development of a hypocone is a derived feature for only some taxa within the Caniformia.

Tedford (1976, p. 372) considered the development of a teres process and postscapular fossa on the scapula to be derived for the Arctoidea. He also discussed the morphology of the scapula in "pinnipeds" and arctoids and concluded that the Otarioidea were most closely related to the Ursoidea, and the Phocidae were most closely related to the Mustelidae within the Arctoidea. Details of the scapular morphology indicated that the otarioids and phocids are very differently derived in their shoulder girdles even though both groups are aquatically adapted. Davis (1949) provided a detailed discussion of the shoulder architecture of a number of living carnivorans. This study concluded that the teres major process was relatively large to very large in procyonids and ursids, and absent in canids and felids (no "pinnipeds" were considered).

Our study indicates that the development of a large teres major process is more common in the Carnivora than was originally indicated by Davis (1949) and Tedford (1976), and that this feature may be derived for the

Caniformia. Within the Carnivora *Oödetes*, *Vulpavus*, the Amphicyonidae, Nimravidae, and Arctoidea all possess a large teres process on the scapula. The Canidae, *Palaeogale*, and all Feloidea lack a teres process (the scapula is unknown in any early Tertiary Feliformia); in these forms the teres major origin is marked only by a scar on the axillary border near the vertebral angle (Davis, 1949, p. 285).

The preserved scapulae of *Vulpavus* (AMNH 11498) and *Palaeogale* (AC 22-2012) are both broken, but enough of the infraspinous fossa and axillary border are present to indicate the presence or absence of the teres process in each. *Palaeogale* agrees well with all other known feliforms in possessing a scapula with a straight axillary border and no indication of a teres process. *Vulpavus*, however, has a moderately large teres major process that is similar in size to the process found in many procyonids. A small, vertical rib separates the infraspinous fossa from the teres process in *Vulpavus*. *Oödetes* also has a large teres process and a small bony rib separating the teres process from the infraspinous fossa (see Matthew, 1909, p. 378).

Members of the Amphicyonidae (Caniformia) have a very large teres process that is separated from the infraspinous fossa by a large secondary scapular spine (see Olsen, 1960, p. 8, fig. 6, and pl. 1; Peterson, 1910, pp. 231–232, pls. 78, 83 and 84; Bergounioux and Crouzel, 1973, fig. 47). This resembles the scapular morphology of the Ursidae, Otariidae, and Phocidae within the Arctoidea. The Procyonidae (Arctoidea) have a smaller teres process, but they lack a secondary scapular spine. Within the Procyonidae the teres major process is generally “relatively large and plate-like” (Davis, 1949, p. 293) as in *Bassariscus*, *Nasua*, and *Procyon*.

The Nimravidae (here considered Caniformia, see below) have a teres major process that is very broad and large in *Hoplophoneus* (see Osborn, 1910, fig. 87 and Hough, 1950, pls. 27–29) and *Dinictis* (AMNH 38805, and see Matthew, 1901b, pl. 38). In both of these genera there is a well-developed bony rib

separating the teres process from the infraspinous fossa.

Most other mammals lack an enlarged teres process and development of a secondary scapular spine. The primitive condition for the Theria is a scapula with a relatively straight axillary border, no teres major process and a single scapular spine separating the infraspinous fossa from the supraspinous fossa. Anteaters and armadillos, however, parallel some Carnivora in the development of a huge teres process and secondary scapular spine, presumably as an adaptation for digging (see Davis, 1949).

The wide distribution of the teres major process within the primitive and derived members of the Caniformia, and its absence in most other mammals, leads us to conclude that this is a derived feature for the Caniformia. All known Feliformia lack any indication of a teres major process or a secondary scapular spine. The Canidae, however, parallel the Feliformia in the lack of a teres major process; presumably this is a secondary loss within the canid caniforms.

The Caniformia retain all the primitive carnivoran features mentioned in the diagnosis of the suborder. These characters have been discussed in earlier sections of this paper, and are not considered further here. The list of characters primitive for the Caniformia is provided in the diagnosis as an aid in characterizing members of the suborder, and as a hypothetical morphotype to assist in the determination of character polarities within the Caniformia.

A number of taxa that were previously allied with taxa we place in the Feliformia have been excluded from the suborder because of their lack of the derived features uniting the Feliformia. These non-feliform taxa appear to belong in the Caniformia, instead, as they share the derived characters of the caniforms. Included within this group of controversial taxa are *Oödetes*, *Plesiomiakis*, *Quercygale* and the Nimravidae. All of these taxa are more thoroughly discussed below.

FAMILY NIMRAVIDAE COPE, 1880b

DISCUSSION: The distinction of two major groups in the Felidae has been established

by numerous workers (for example, Cope, 1880b; Teilhard de Chardin, 1915; Piveteau, 1961; de Beaumont, 1965). We recognize the nimravids or "paleofelids" as a separate group of carnivores having nothing to do directly with the phylogeny of the true cats (or neofelids). The "paleofelids" are not members of the Felidae, they are excluded from the Feloidea (Felidae, Viverridae, and Hyaenidae), nor can they even be considered members of the Feliformia, as constructed in this paper. In addition, the distinction of the Nimravinae and Hoplophoneinae as two distinct, recognizable groups of "paleofelids" by de Beaumont (1964) appears to be valid here, and the two lineages are considered subfamilies of the family Nimravidae. We follow Tedford's (1978) resurrection of the family Nimravidae to include both the Nimravinae and the Hoplophoneinae. Martin (1980) and Baskin (1981) also recognize the Nimravidae, and include in this family de Beaumont's Nimravinae and Hoplophoneinae.

The "paleofelids," which include *Dinictis*, *Pogonodon*, *Nimravus*, and *Dinaelurus* in the Nimravinae, and *Hoplophoneus*, *Eusmilus*, *Sansanosmilus*, and *Barbourofelis* in the Hoplophoneinae, have generally been considered by previous workers to be members of, or close allies to, the Felidae. Analysis of dental characters, and the subsequent construction of a cladogram based on these data, indicate that the Nimravidae are not members of the Feliformia clade. All nimravids lack the diagnostic, well-developed parastyle on P⁴ and the slitlike form of the metastyle notch on P⁴ that are found in all feliforms.

The parastyle is very poorly developed or absent in all nimravids except *Barbourofelis* in which a large "parastyle" is developed in much the same manner as in various sabretoothed neofelids. Some nimravids (e.g., *Nimravus*) have a deep groove high on the strong ridge running anteriorly from the apex of the paracone, resulting in a cusplike structure just anterior to the groove. This structure is positioned much higher on the flank of the paracone than would be a true cingular parastyle cusp, and it appears obvious that

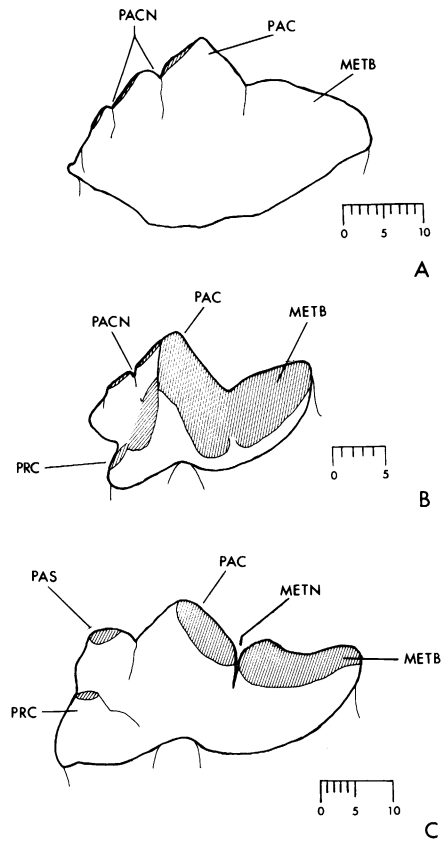


FIG. 9. Comparison of P⁴ morphology in the Nimravidae and the Feloidea. A) *Barbourofelis* (AMNH 61895), B) *Hoplophoneus* (AMNH 69417), and C) *Crocuta* (AMNH Comparative Anatomy Collection 27765). All views are lingual, scales in millimeters. PACN—notch in paracone ridge; all other abbreviations as in figure 1.

these two structures are not homologous (see fig. 9). The condition in *Barbourofelis* seems to be an elaboration of the anterior paracone ridge and groove found in *Nimravus* and *Hoplophoneus*, which results in a superficial similarity to the large, true parastyle incorporated into the shearing blade of *Smilodon*.

Furthermore, the structure of the broad, deep, rounded groove in *Barbourofelis* is distinctly different from the very narrow, sharp, slitlike notch between the parastyle and paracone in sabretoothed neofelids. *Barbourofelis* and other nimravids also lack the deep, sharp notch in the metastyle blade;

they have a shallower, broader, grooved notch that does not extend dorsally as a slit in the crown.

The Nimravidae also have the weak, anteriorly located protocone on P^4 that is characteristic of the Caniformia. Although the protocone is most reduced in the more derived Nimravidae (e.g., *Barbourofelis*), this cusp in all nimravids is much smaller than that found in the Feliformia or the eutherian outgroup taxa (see fig. 3). Therefore, the Nimravidae differ from the Feliformia in the reduction of the protocone of P^4 , and instead appear to share this derived feature with other members of the Caniformia.

The Nimravidae lack the calcaneal fibular facet and the articulation between the fibula and the calcaneum. Representative tarsi of the nimravid genera *Dinictis*, *Nimravus*, *Pogonodon*, *Hoplophoneus*, and *Barbourofelis* lack the calcaneal fibular facet and any indication of a facet on the fibula for articulation with the calcaneum. The presence of a large calcaneal fibular facet is primitive for the Carnivora (see discussion in the Carnivora section, above). A large facet is found in the primitive feliform *Didymictis* and a smaller facet is present in many living Viverriidae. The loss of this calcaneal fibular facet is surely derived, and it appears to be a shared derived feature uniting the Nimravidae with all other Caniformia.

The presence of a large teres major process separated from the infraspinous fossa by a bony ridge, in all Nimravidae for which a scapula is known, is a derived feature uniting the Nimravidae with the Caniformia. This feature is found throughout primitive and derived Caniformia taxa, is only rarely observed in non-carnivoran mammals (see discussion in Caniformia section), but is never present in any Feliformia. This derived scapular morphology supports exclusion of the Nimravidae from the Feliformia and placement of the family within the Caniformia, instead.

Cranial evidence strongly supports the separation of the Nimravidae from the Feloidea, and further corroborates the hypothesis that they are members of the Caniformia that resemble certain felids only through

convergence in the dentition. Hough (1953) proposed a superfamily Cynofeloidea to include the Canidae, the Felidae and the Nimravinae (considered a subfamily of the Felidae). This was based on a belief that the nimravines represented morphological intermediates between the Felidae and Canidae, in which the dentition resembled that of the neofelid "sabretooths" and the basicranium was much more similar to the Canidae. Any similarities between the Felidae and other Aeluroidea were assumed to be the result of convergence. It may also be inferred, here, that if the ancestral felid morphology was represented by the nimravines (as indicated in the Hough, 1953 phylogeny), then neofelids lacking smilodonty secondarily evolved a less derived dental morphology. Just such a phylogeny and morphocline polarity was more explicitly presented by Matthew (1910a) in his discussion of the phylogeny of the Felidae.

Hough's (1953) alliance of the Nimravinae with the Canidae, or at least the Caniformia of this paper, is here considered valid. The use of this group as a morphological "bridge" between the Canidae and true Felidae is unacceptable, however, as it is based solely on dental characteristics that are convergent, demands secondary reversal and simplification of dental morphology within some Felidae, and requires ad hoc assumptions of convergence in dental and basicranial features between the Felidae and other Feloidea.

If the Nimravidae (including *Hoplophoneinae*) are hypothesized as Feliformia, their lack of a fully ossified, true septum bullae and the presence of a postglenoid foramen excludes them from a phyletic position within the Feloidea, represented by the trichotomy of the Felidae, *Hyaenidae* and *Viverriidae* at Node 10 of the cladogram (fig. 4). The basicranial foramina, and the inferred circulatory pattern, further support the exclusion of the Nimravidae from the Feloidea. Nimravid basicrania are generally more canoid in arrangement and are strikingly different from the derived pattern found in true felids.

Hough's (1953) extensive analysis of the auditory region in fossil Felidae (which in-

cluded taxa presently considered "paleofelids" *Hoplophoneus*, *Eusmilus*, *Dinictis*, and *Nimravus* and the neofelid genus *Smilodon*, which was considered a "paleofelid") presented evidence that the ear region in "paleofelids" was distinctly canoid in structure and pattern. Hough stated that the bulla is never completely ossified and it lacks any trace of a true septum bullae (although *Barbourofelis*, a derived hoplophoneine unknown to Hough, does have a completely ossified bulla and internal bony struts, but no septum bullae).

Baskin (1981) discusses the "septum bullae" in the Nimravidae, as well as its role in the classification of the Carnivora. Baskin cites work by Clark and Guensburg, and Brunet, as well as his own observations, documenting the presence of what they consider a septum in the bullae of *Dinictis* and *Hoplophoneus*. These workers have not convincingly supported the assertion that there is a complete septum in the bulla of any nimravid. We do not believe that there is a true septum in the bulla of any Nimravidae that would be homologous with the septum in either the Canidae or the Felioidea. Martin (1980, p. 152) also states that "No septum bullae occurs in any paleofelid, including *Barbourofelis*." The development of a bony outgrowth in the bullae of the Nimravidae may correspond in topographic position to the complete septum found in the Canidae, and its presence and precise location of development within the bulla may be a derived feature uniting the Nimravidae and the Canidae.

The basicranial foramina were shown (Hough, 1953, p. 99) to be distinctly different from the pattern and numbers found in the feloids, and to much more closely resemble the canoid condition. Some of these characters, however, may be primitive for all the Carnivora. An alisphenoid canal, large postglenoid foramen, large condyloid foramen separate from the foramen lacerum posterius, and a large carotid canal are all found in the Nimravidae and many Caniformia, but are absent or modified differently in all Felioidea. The living and most fossil Felidae are extremely different in the lack of an alisphenoid

canal, the close connection or confluence of the condyloid foramen and the foramen lacerum posterius, and the extreme reduction in size of the carotid canal.

Work presently in progress by N. Neff and R. Tedford on the basicrania and carotid circulation of the Nimravidae should provide important new information relevant to the determination of the phyletic relationships of this group.

The striking morphological differences between the basicrania of the Nimravidae and the true Felidae, and the lack of any derived felid characters in the Nimravidae, precludes a close relationship between the two groups. Since the Nimravidae are not members of the Felidae, any dental features in common (hypercarnivory, smilodonty, etc.) must have been evolved independently and convergently in the two lineages. If indeed the Nimravidae are convergent with the Felidae, then that similarity may have evolved at any point in the phyletic lineage of the Carnivora. No longer must we consider the nimravids as close relatives of the cats. Instead, the morphological evidence from the basicrania and the dentition strongly indicates an association of the Nimravidae with the Caniformia, rather than with the Aeluroidea. We advocate removal of the Nimravidae from the Feliformia, altogether, and alternatively hypothesize a relationship with the Caniformia. All previous workers have considered the nimravids as ancestors, or very close relatives, of the Felioidea. We believe that the lack of any of the derived features of the Felioidea or Feliformia excludes the Nimravidae from a phyletic position within these groups. The Nimravidae are a very specialized group representing a divergent lineage within the Caniformia. A determination of the precise phyletic position of the Nimravidae within the Caniformia awaits a more detailed analysis of this group.

Oödictes Wortman, 1901

DISCUSSION: *Oödictes* was proposed by Wortman (1901) as a new genus within the

Viverravidae, but was later moved by Matthew (1909) to a position within the Miacinae. Simpson (1945) followed Matthew's work and included *Oödetes* within the Miacinae.

The precise systematic position of *Oödetes* is debatable, but we include it within the Caniformia. The presence of three molars excludes *Oödetes* from the Feliformia, as here defined, but this primitive retention does not necessarily ally it with the Caniformia. *Oödetes* has a moderately well-developed basal P⁴ parastyle, but it is not as enlarged as in other primitive feliforms, nor as reduced as in some caniforms. This morphology may represent a retention of the primitive carnivoran (and eutherian) condition, the most primitive elaboration of the feliform parastyle, or the least reduction of the parastyle within the Caniformia lineage. The lack of a hypocone in *Oödetes* is irrelevant, as not all caniforms develop molar hypocones. The lingual molar cingulae are moderately well-developed, and may be only weakly continuous around the base of the protocone. Again, this represents the primitive morphology and does not ally the genus with the Feliformia, but would make it a very primitive caniform if it were included within the Caniformia. However, as mentioned above, other Caniformia have only a very weak development of the continuous lingual cingulum, and these forms do not appear to be significantly more advanced than *Oödetes* in this trait. *Oödetes* is more similar to the Caniformia in the presence of a reduced P⁴ protocone and in the shallowness of the carnassial notch on P⁴. The talonid of M₂ is short in *Oödetes*, and is never as enlarged as in the Feliformia. The hypoconulid is smaller than the hypoconid on M₂, as in the Caniformia and outgroup taxa, and not expanded in size as in the Feliformia. Presence or absence of the fibulo-calcaneal facet cannot be determined in *Oödetes*.

The scapula of *Oödetes* has the large teres process and secondary scapular rib that is a derived feature found in all Caniformia (see discussion in Caniformia section, above).

Xinyuictis tenuis Zheng, Tong and Ji, 1975,

from China⁹ is very similar to *Oödetes* in both size and morphology. This genus also appears to belong in the Caniformia. It has a short M₂ talonid, very high M₂ trigonid, M₂ hypoconid larger than the hypoconulid, and the parastyle of P⁴ is a weak, low elaboration of the cingulum and not well developed as a cusp; all of these primitive characters are variably modified in the Feliformia. Furthermore, *Xinyuictis* has the reduced P⁴ protocone and lingual upper molar cingulum continuous around the base of the protocone that are diagnostic for the Caniformia. The presence or absence of M₃ in *Xinyuictis* is not known from the presently available material, but in most other features the dentition of this genus closely resembles *Oödetes*, and the two may be closely related taxa.

MacIntyre and Guthrie (1979) have recently expanded the hypodigm of *Oödetes* by synonymizing *Paeneprolimnocyon* with *Oödetes*. All the material of the type species, *P. amissadomus* was included within the only species of *Oödetes*, *O. herpestoides*.

Oödetes appears to lack most of the derived features of both the Caniformia and the Feliformia. Due to the lack of any definitive synapomorphies between *Oödetes* and the Feliformia, and the presence of a reduced P⁴ protocone, large teres process on the scapula, and a weakly continuous lingual cingulum on the molars of *Oödetes*, we consider the genus a member of the Caniformia.

"*Plesiomiakis*" (Stock, 1935)

DISCUSSION: *Plesiomiakis* Stock, 1935, originally described as a subgenus of *Viverravus*, was recognized by Simpson (1945) as a distinct genus in the "Viverravinae." In this context *Plesiomiakis* extended the temporal range of the "Viverravinae" into the late Uintan. The phyletic position of *Plesiomiakis progressus* proposed by Stock and

⁹ Casts of the genus are housed in the American Museum of Natural History and Museum of Paleontology, Michigan.

Simpson is erroneous. *Plesiomiakis* is not closely related to *Viverravus*, nor can it be considered a "viverravine" feliform; instead, it is definitely a "miacine" caniform.

Plesiomiakis has the reduced P^4 protocone and parastyle, and continuous lingual cingulum on the upper molars that are diagnostic for the Caniformia, and lacks all the features diagnostic for the Feliformia (except for a presumed analogous loss of M_3^3).

Plesiomiakis is extremely similar morphologically to the caniform *Procynodictis*, differing only in very minor details of the teeth and in the absence of M_3 (and presumably M^3 , also). The premolars are very similar in both genera, as are the molar trigonids. The molar talonids are slightly different, but both genera have a trenchant cristid obliqua and a moderately developed lingual basin on the talonids. *Plesiomiakis* and *Procynodictis* share a distinctive M^1 morphology in which the parastyle wing is long and narrow, paracone is on the anteriormost edge of the tooth and widely separated from the metacone, lingual portion of the tooth is slightly to moderately more narrow than the buccal part, hypocone is moderately well developed as a distinct cusp, all the cingulae (especially the anterior cingulum at the base of a straight anterior margin) are reduced, conules (particularly the metaconule) are reduced or absent, and the paraconule and metaconule cristae are also reduced. P^4 and M_2 in both genera are typically caniform in the very short M_2 talonid length, P^4 protocone reduced and far forward, and presence of a very small basal parastyle. M^3 may already be absent in *Procynodictis* (although this cannot be determined with certainty), and M_3 is very reduced. The characters cited by Stock (1935) to distinguish *Plesiomiakis progressus* from *Viverravus* are all shared with *Procynodictis*. Therefore, although *P. progressus* is probably a species distinct from *Procynodictis vulpiceps*, it is doubtful that *P. progressus* should be considered generically distinct solely on the basis of the loss of M_3 .

Van Valen (1967) first recognized that the absence of M_3 did not exclude a species from

a position within the "Miacinae," nor did it necessarily require inclusion within the "Viverravinae." This was based on the synonymy of *Quercygale* (a supposed "viverravine" lacking M_3) with *Tapocyon* (a "miacine" that retained M_3). Therefore, Van Valen assumed that the lack of M_3 was not confined exclusively to the "Viverravinae," and that advanced species of true "Miacinae" could lose M_3 in parallel. This is correct, and *Plesiomiakis* represents another illustration of this situation. Careful and rigorous analysis of character distributions in these taxa, indicates that they can all be assigned to the Caniformia; both *Plesiomiakis* and *Quercygale* lack the defining synapomorphies of the Feliformia and possess those that characterize the Caniformia, instead. Even if both *Plesiomiakis* and *Quercygale* were considered generically distinct from *Procynodictis* and *Tapocyon*, respectively, they may still be considered caniforms that are more derived than most other early Tertiary caniforms in the loss of the primitively retained M_3 . Simpson (1946) provides a similar discussion of the reasons for not assigning generic value to differences in the presence or absence of a very reduced tooth between otherwise very similar taxa.

In any case, the occurrence of "*Plesiomiakis*" does not extend the temporal range of the "Viverravinae" (primitive Feliformia) into the late Uintan of North America. "*Plesiomiakis*" is a member of the Caniformia, included in the genus *Procynodictis*, and is not closely related to the members of the Feliformia.

Quercygale Kretzoi, 1945

DISCUSSION: Both Van Valen (1967) and de Beaumont (1965) recognized the resemblance of *Quercygale* ("*Humbertia*" of de Beaumont, 1965) to *Tapocyon*. Van Valen believed that *Quercygale* was either synonymous with or should be considered a subgenus of the "miacine" *Tapocyon*, whereas de Beaumont retained "*Humbertia*" in the "Viverravinae." We believe that *Quercy-*

gale is not closely related to the feliforms with which the genus was previously classified within the "Viverravinae," that it is definitely a member of the Caniformia, and that the genus may be closely related to *Tapocyon* and *Uintacyon*.

Quercygale has the very reduced P⁴ parastyle and protocone, and a weak, but continuous, lingual cingulum on the upper molars, which are diagnostic features for the Caniformia. Furthermore, *Quercygale* lacks all of the derived features for the Feliformia, except for the loss of M₃³. *Quercygale* retains primitive carnivoran features such as a short, unexpanded M₂ talonid; M₂ hypoconid larger than the hypoconulid; P⁴ metastyle notch only moderately deep and narrow; a large, anteromedially located postglenoid foramen; and an unossified bulla. This suite of characters indicates that *Quercygale* is certainly a caniform, although in many features it is more derived than many other early Tertiary caniforms, and parallels some other caniforms in the loss of M₃³.

Quercygale is morphologically similar not only to *Tapocyon*, as was recognized by other workers, but to *Uintacyon* as well. *Quercygale* appears to be closely related to either one, or both, of these genera. *Quercygale* resembles *Uintacyon* in the general outline of P⁴, M¹, and P₄; the position of the talonid cusps on the buccal margin of P₄, and the development of a large, lingual basin; the closed-V formed between the paralophid and protolophid of M₁; and many features of M¹, such as weak lingual cingulum, lack of metaconule, weak parastyle "hook" and strong development of the metastyle, etc. Alternatively, *Quercygale* resembles *Tapocyon* in the development of an M₁ metaconid > paraconid size; anteroposterior alignment of the cristid obliqua of M₁; outline of M₁; and development of a pronounced flange at the anterior end of the mandible. Some of these resemblances may only be shared primitive features and would not be indicative of any special relationship between the various taxa. Also, in many features *Tapocyon* appears to be more derived than both *Uintacyon* and *Quercygale*. These include the development of a relatively large, robust,

bladelike P₄ anterior accessory cusp; open M₁ trigonid-V; great reduction of M₂; strong lingual cingulum on M¹; and large, "hook"-shaped blade on the parastyle of M¹.

PHYLOGENY OF THE CARNIVORA

The following list of characters abstracts the features that are assumed to be derived for the members of each taxon. The nodes are those given in the phylogeny of figure 4.

Node 1: Order Carnivora

- A) P⁴/M₁ modified as principal carnassial teeth, lacking a migratory locus for the carnassial
- B) P⁴ protocone located anterolingually, far forward of the paracone
- C) extremely well-developed, elongate P⁴ metastyle wing with a well-developed metastyle blade and carnassial notch
- D) well-developed, elongate P₄ talonid with at least two posterior accessory cusps
- E) M₂₋₃²⁻³ reduced in size
- F) processus hyoideus formed by a ventromedial prolongation of the squamosal.

Node 2: Suborder Feliformia

- A) P⁴ parastyle enlarged
- B) very deep, narrow, slitlike carnassial notch in the metastyle blade of P⁴
- C) M₃³ lost
- D) M² reduced in size, simple in morphology
- E) M₂ talonid extremely elongate; tooth with elongate oval outline
- F) M₂ hypoconulid larger than, or equal to, hypoconid size.

Node 3: Infraorder Didymictida (Family Didymictidae)

- A) M₂ paraconid extremely, and metaconid moderately, reduced; paraconid much smaller than or subequal to metaconid size
- B) well-developed notch between anterior accessory cusp and main cusp on P₄
- C) P₄ talonid broad
- D) canines multigrooved.

Node 4: *Protictis*

- A) anterior accessory cusp on P₄ enlarged and very high

- B) lingual margin of P_4 anteroposteriorly straight
- C) P^3 develops a weak, but distinct, protocone cusp anterior to the paracone apex
- D) P_4 main cusp situated on buccal tooth margin
- E) main cusp on P_4 leaf-shaped in lateral outline.

Node 5: *Protictis* (*Bryanictis*)

- A) P_4 anterior accessory cusp tremendously enlarged and modified for shearing
- B) expansion and very deep basining of lingual portion of P_4 talonid
- C) large, well-developed P^3 protocone
- D) all P_4 cusps very strongly laterally compressed
- E) alignment of P_4 cusps in a straight, anteroposterior line on buccal tooth margin; buccal tooth margin anteroposteriorly straight.

Node 6: Unnamed taxon (*P.* (*Protictis*) and *P.* (*Protictoides*))

- A) buccal margin of P^4 straight
- B) P^4 cusps compressed and trenchant
- C) P^4 parastyle extremely large, higher relative to protocone
- D) deep second posterior notch between enlarged first and second posterior accessory cusps on P_4 .

Node 7: Infraorder Aeluroida

- A) conules absent on upper molars
- B) M_1 paraconid and metaconid far separated, resulting in an open-V between the paralophid and protolophid on the trigonid
- C) loss of the second posterior accessory cusp on P_4 ; talonid simpler
- D) reduction of molar cingulae.

Node 8: Superfamily Viverravoidea

- A) paroccipital process extremely reduced
- B) supraoccipital process extremely reduced
- C) postglenoid foramen located far posteroexternally on the postglenoid process of the squamosal.

Node 9: Family Viverravidae

- A) P_4 anterior accessory cusp far anterolingual on crown

- B) M_2 talonid extremely elongate; hypoconulid large and bulbous with anterior occlusal facet
- C) anterobuccal basal trigonid cingulum on M_1 weak
- D) M_1 hypoconulid strong, posterocentrally located, and projecting posteriorly from talonid margin
- E) anterior trigonid notch on M_2 reduced, resulting in a continuous, low paralophid.

Node 10: Superfamily Feloidea

- A) ossified, bipartite bulla with a large ectotympanic septum
- B) great reduction or loss of the postglenoid foramen
- C) scaphoid and lunar united in a single scapholunar bone
- D) paroccipital process broadly based and closely appressed to the posterior wall of the bulla
- E) development of an intracranial arterial rete in the orbital region, internal carotid artery reduced in size or vestigial.

Node 11: Suborder Caniformia

- A) loss of calcaneal fibular facet in the pes
- B) great reduction or absence of the parastyle on P^4
- C) reduction in size of the P^4 protocone
- D) lingual cingulum on upper molars complete around the protocone base
- E) large teres major process on the scapula.

CHARACTER CONTRADICTIONS

The following list is a summary of the distribution of characters that contradict the phylogenetic arrangement proposed above:

1) reduction of P_4 talonid to one posterior accessory cusp—*Didymictis*, Aeluroida, some early and late Tertiary Caniformia.

2) ossified, single scapholunar bone—Feloidea, some *Vulpavus* (see Matthew, 1909), *Vassacyon* (Matthew, 1915, p. 40), *Procyonodictis* (Wortman and Matthew, 1899, p. 122), and late Tertiary Caniformia.

3) completely ossified bulla—*Palaeogale*, Feloidea, late Tertiary Caniformia.

4) enlargement of anterior accessory cusp on P_4 —*Protictis*, *Tapocyon*.

5) M_3^3 lost—Feliformia, and some derived members of the Canidae, Procyonidae, Mustelidae, Nimravidae, *Quercygale*, and “*Plesiomiacis*” (within the Caniformia).

6) conules absent on upper molars—Aeluroida, some late Tertiary Caniformia.

7) great reduction or loss of the postglenoid foramen—Feloidea, advanced Nimravidae.

8) lingual cingulum on upper molars complete around the base of the protocone—Caniformia, some *Didymictis*.

9) loss of the calcaneal fibular facet in the pes—Caniformia, some Feloidea.

10) open trigonid-V on M_1 —Aeluroida, some Caniformia.

Characters 1–3 are found in all the later Tertiary Carnivora, and 2–3 have traditionally been used to unite Simpson’s Feloidea and Canoidea and to exclude the “Miacoida.” Of these, however, only the complete ossification of the bulla unambiguously supports the traditional grouping of the Canoidea and Feloidea to the exclusion of the “miacids.” All the characters other than the ossified bulla have a variable distribution throughout both the early and later Tertiary Carnivora. The sporadic distribution of these characters contradicts some of the relationships hypothesized in the phylogeny outlined above, but does not reasonably support the traditional, or any other alternative, phylogeny for the Carnivora. The contradictions cited here highlight features that may have evolved convergently in various canivoran taxa, and suggest future areas of investigation of the supposed homologies and distributions of these morphological characters.

CLASSIFICATION

The following classification was constructed to be consistent with the phylogeny presented above and in figure 4. The classification does not precisely reflect the detail of relationships portrayed in the cladogram; instead, an attempt is made to minimize the proliferation of new taxa, retain previously

named taxa when possible, and to maintain logical consistency between the phylogeny and the classification.

Order Carnivora Bowdich, 1821

Suborder Feliformia Kretzoi, 1945

Infraorder Didymictida, new

Family Didymictidae, new

Didymictis Cope, 1875

Protictis (Matthew, 1937)

P. (*Protictis*) (Matthew, 1937)

P. (*Protictoides*), new

P. (*Bryanictis*) MacIntyre, 1966

Infraorder Aeluroida, new

Superfamily Viverravoidea Wortman and Matthew, 1899

Palaeogale von Meyer, 1846

Family Viverravidae Wortman and Matthew, 1899

Viverravus Marsh, 1872

Simpsonictis MacIntyre, 1962

Superfamily Feloidea Hay, 1930

Infraorder Aeluroida, *incertae sedis*

*Ictidopappus*¹⁰

Suborder Caniformia Kretzoi, 1943

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¹⁰ The *incertae sedis* placement of *Ictidopappus* within the Aeluroida indicates that the genus shares all the derived features of the infraorder, but that the Viverravoidea and Feloidea do not share any features that exclude *Ictidopappus*. Further, neither of the aeluroid superfamilies have uniquely derived features that are known to exclude *Ictidopappus* from these taxa. Therefore, the precise phyletic position of *Ictidopappus* is uncertain; the genus may potentially be most closely related to either, or both, of the superfamilies, or even have a position within either superfamily.

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