MIDDLE MIOCENE CARNIVORA OF NEW MEXICO (TESUQUE FORMATION): SPECIES PATTERNS, RICHNESS, AND FAUNAL TURNOVER

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Abstract—Recent field work and research call for a new look at the carnivorans from the middle Miocene of New Mexico. Here changes in carnivoran guilds through time within the Tesuque Formation as well as the carnivoran diversity in each member are described. The Tesuque Formation in New Mexico contains fossiliferous layers of strata that span the late Hemingfordian through the Clarendonian (and potentially into the earliest early Hemphillian). Borophagines were the dominant carnivorans, and presumably the dominant predators, during the middle Miocene in New Mexico. However, when borophagines become less abundant, canines become more abundant, showing an inverse relationship and perhaps leading to instances where members of these groups utilize similar niches. Hesperocyonines are only present in the early Barstovian, while the large amphicyonids are found only in the late Barstovian, potentially filling an open niche left by the hesperocyonines. While carnivoran diversity drops after the Barstovian, mustelids persist in the early Clarendonian. Felids tend to become less numerous through time, perhaps allowing mustelids to fill the role of the small predators in place of *Pseudaelurus* (among others), and these may have in turn been replaced by small canines. In addition, this study records the first occurrences of several carnivorans in distinct members, or in the Tesuque Formation as a whole, including the first occurrence of mustelids (non-mephitine mustelids) in the formation. While the carnivoran fauna from the middle Miocene of North America is more diverse, it is noted that the Tesuque carnivoran fauna has a higher percentage of canids, and a lower percentage of mustelids and procyonids. Statistical analyses show each carnivoran group is found in most of the members and so do not cluster differently with the exception of Hesperocyoninae. The Barstovian Skull Ridge and Pojoaque members are the most statistically similar in terms of their carnivoran diversity.

INTRODUCTION

The Santa Fe Group (Spiegel and Baldwin, 1963) was comprehensively collected and sampled for vertebrate fossils by the American Museum of Natural History (AMNH) between 1924 and 1960 (see Galusha and Blick, 1971). Although collecting to a lesser degree has continued since 1960 (e.g., Aby et al., 2011), the majority of Tesuque Formation fossils in museum collections today are still housed at the AMNH. Indeed, many of the Santa Fe Group vertebrate fossils collected by the American Museum of Natural History are part of the Frick Collection. A relatively small portion of this collection has been formally catalogued (see Kues and Lucas, 1979), and even less has been published on these fossils. The Tesuque Formation, in particular, is one of the best sampled stratigraphic units for vertebrate fossils from the Miocene of North America. In addition to the fossils that are part of the Frick Collection, the New Mexico Museum of Natural History and Science (NMMNH) has been conducting supplementary collecting trips, and their collection of carnivoran fossils from the Santa Fe Group, and the Tesuque Formation in particular, is growing (e.g., Aby et al., 2011). Indeed, due in large part to the collecting in the early to mid 20th century, a large number of carnivoran (Carnivora) fossils are known from the Miocene, and in particular the middle Miocene, of New Mexico.

Carnivorans from the Tesuque Formation have been known for over 130 years (e.g., Cope, 1874). However, even with the large number of carnivoran specimens known from the Tesuque Formation, relatively few studies have been published on this material, or have noted their presence (e.g., Cope, 1874, 1877; Frick, 1926; Wang, 1994; Baskin, 1998a, 1998b; Hunt, 1998a, 1998b; Munthe, 1998; Wang et al., 1999; Rothwell, 2001, 2003; Chaney, 2009; Tedford et al., 2009; Aby et al., 2011; Jasinski and King, 2014).

The Tesuque Formation, and its stratigraphy, have been the subject of multiple studies (e.g., Spiegel and Baldwin, 1963; Galusha and Blick, 1971; Kues and Lucas, 1979; Tedford and Barghoorn, 1993, 1997; McKinney et al., 2001; Koning et al., 2005; Aby et al., 2011). Galusha and Blick (1971) divided the Tesuque Formation into five members: Nambé, Skull Ridge, Pojoaque, Chama-El Rito, and Ojo Caliente members (Fig. 1). There have been other smaller and less extensive members defined within the Tesuque Formation, including; the Dixon (Steinpress, 1980, 1981), Cieneguilla (Koning et al., 2004), and Cejita (Manley, 1977) members (see Aby and Koning, 2004). While all three of these members are more restricted in their outcrops, a single carnivoran specimen has been collected from the Dixon Member

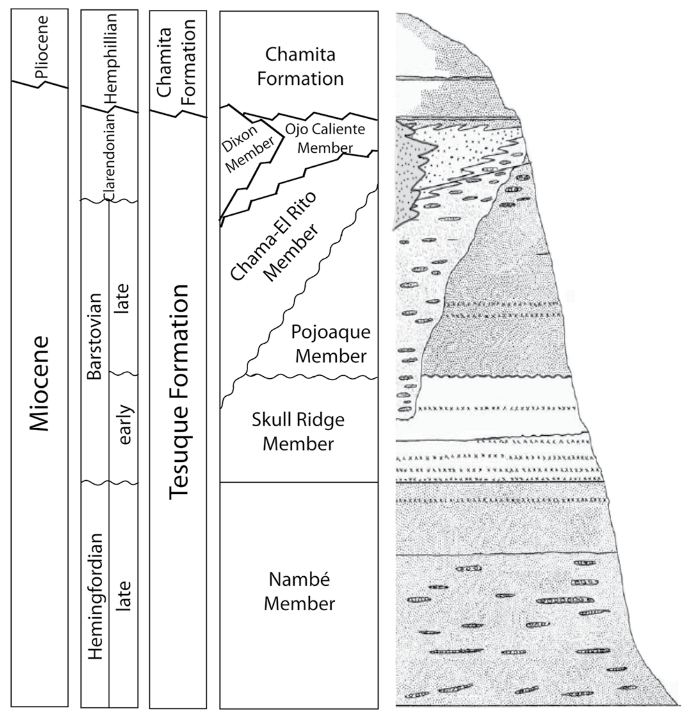

FIGURE 1. Generalized stratigraphy of the Tesuque Formation. Modified from Galusha and Blick (1971) and Aby and Koning (2004).

(*Aelurodon taxoides*, see Wang et al., 1999), so this member was included in the present study for completeness (Fig. 1).

As the Tesuque Formation is one of the best sampled middle Miocene units in North America and supplemental collecting has provided more carnivoran fossil specimens, it provides a key unit for studying carnivorans from the middle Miocene of North America. Due to the faunal richness of this region and its association with the mid-Miocene climatic optimum, further analysis of the carnivoran fauna and its dynamics could potentially be important and informative.

Specifically, I sought to investigate carnivoran faunal dynamics, including carnivoran faunal patterns, taxonomic turnover, and faunal richness. I also sought to examine and compare patterns within the Tesuque Formation, and compare the overall pattern with that of the rest of North America.

Institutional abbreviations: AMNH, Department of Vertebrate Paleontology, American Museum of Natural History, New York, New York; **F:AM**, Frick Collection, Department of Vertebrate Paleontology, American Museum of Natural History, New York, New York; **NMMNH**, New Mexico Museum of Natural History and Science, Albuquerque, New Mexico; **USNM**, United States National Museum of Natural History, Smithsonian Institution, Washington, D.C.

METHODS

All members of the Tesuque Formation were investigated to find all carnivoran fossils known from the formation. The majority of the fossils collected are part of the famous Frick Collection housed at the AMNH and represent larger, more complete specimens. I collected NISP (number of individual specimens) data from the number of recorded specimens collected from the Tesuque Formation that were housed in the AMNH, NMMNH, and USNM collections and from previously published data (e.g., Wang, 1994; Baskin, 1998a, 1998b; Hunt, 1998a, 1998b; Munthe, 1998; Wang et al., 1999; Rothwell, 2001, 2003; Chaney, 2009; Tedford et al., 2009; Aby et al., 2011). All the fossil-bearing members of the Tesuque Formation were included in the statistical analyses, except the Dixon Member (Nambé, Skull Ridge, Pojoaque, Chama-El Rito, and Ojo Caliente) (Fig. 1). Only a single carnivoran taxon is represented in the Dixon Member, and as such it would not have been as statistically significant in comparison to the more richly-fossiliferous members. Over 300 carnivoran specimens (n=342 total) from the Tesuque Formation were identified and used for this study (see Appendix).

Carnivoran taxonomic groupings were maintained on the subfamily level whenever possible (Table 1), except in the case of the Mustelidae and Felidae (see discussion of the latter families below). Indeed, as the subfamily of *Pseudaelurus* is uncertain, Felidae was maintained as a taxonomic group, although it only contains *Pseudaelurus* and the species within. NISP data were used, along with percentages of each group within the different members and ages.

As the Skull Ridge (early Barstovian) and Pojoaque (late Barstovian) faunas were the best sampled of the members of the Tesuque Formation (NISP are 78 and 216, respectively), I compared their faunas directly to investigate changes in the carnivoran fauna during the Barstovian in New Mexico. Additionally, data from the Paleobiology Database (www.fossilworks.org) were used to compare the middle Miocene carnivoran fauna of New Mexico (i.e. the Tesuque Formation) with that of North America. For each of these, ratios were created for the number of specimens from each taxonomic grouping compared to the total NISP from the Skull Ridge and Pojoaque members. The same was then done for the Tesuque Formation as a whole and for the middle Miocene of North America, with two separate analyses run for the latter, including one for only terrestrial carnivorans and one for all recovered carnivorans.

As another way to investigate taxonomic diversity, rarefaction curves were derived. Rarefaction curves were calculated for members with NISP ≥10 carnivoran specimens and for the Tesuque Formation as a whole. Rarefaction data and curves were derived using the program Analytic Rarefaction 1.3 from Steven M. Holland (2003). The rarefaction equations for the expected number of species (e) were given by Hurlbert (1971) and for the variance of the expected number of species (var) by Heck et al. (1975). Raup (1975) and Tipper (1979) provided additional data for deriving the rarefaction equations used by the program, with the latter, in particular, helping to avoid the overflow errors associated with the large combinatorials. Note that if you test the results of this program by using Table 3 of Raup (1975), the values of var will differ for low values of a range of rarified sample sizes (n) as there was a coding error in Raup's (1975) original program causing his published values of var to be inflated at low values of n (Holland, 2003).

Additionally, a single linkage cluster analysis was run using R on both the taxonomic groups and Tesuque Formation members to investigate faunal similarity. The purpose of the analysis was to determine similarities of taxonomic groupings in NISP through time as well as which Tesuque Formation members had the most similar faunas. To create the cluster analysis, I used Bray-Curtis coefficients, as this calculation is ideal for raw species counts or, in this case, carnivoran taxonomic group abundances. Raup-Crick probability scores (Raup and Crick, 1979) were also calculated for each adjacent member, as well as for the top and bottom of the unit, to determine whether the taxonomic similarities between two members were different than what would be expected at random (α=0.05).

TAXONOMIC GROUPS

Carnivoran taxa were separated into taxonomic groups and subgroups (see Table 1 and below). When possible, taxa were grouped within subfamilies, however with some taxa subfamilies were not certain (e.g., *Miomustela* and *Pseudaelurus*), so higher taxonomic levels (e.g., family level) were used. Many taxonomic identifications were taken from previous studies (e.g., Cope, 1874. 1877; Frick, 1926; Hall, 1930; Wang, 1994; Baskin, 1998a, 1998b; Hunt, 1998a, 1998b; Munthe, 1998; Wang et al., 1999; Rothwell, 2001, 2003; Chaney, 2009; Tedford et al., 2009; Aby et al., 2011). However, not all specimens used in this study had been part of previous studies, and identifications of these specimens were either derived from comparisons or from identifications in museum databases. Differences between large body size and small body size were utilized in a similar way to Carbone et al. (1999) and Werdelin and Lewis (2013), who defined large body size as ≥21.5 kg and small body size as <21.5 kg (Table 1). Carbone et al. (1999) showed that 21.5 kg is a key threshold value for body mass in carnivoran ecology, with those equal to or larger than this value taking large prey (of roughly their own body mass and/or sometimes greater), which Werdelin and Lewis (2013) followed, and which is also followed in the present study.

Carnivora
Caniformia
Amphicyonidae

Amphicyoninae–Amphicyonids, colloquially known as "bear dogs", while rare, make up a significant if small component of the Tesuque fauna. Hunt (1998b) mentioned the presence of the amphicyonines *Amphicyon ingens* and an indeterminate species of *Pseudocyon* (=*Pseudocyon* sp.), while Aby et al. (2011) only mentioned the presence of *Pseudocyon*, in the Pojoaque Member. Both *Amphicyon* and *Pseudocyon* are classified as members of the Amphicyoninae by McKenna and Bell (1997) and Hunt (1998b). While only a few amphicyonid specimens are known from the Tesuque Formation (Pojoaque Member), they would have been some of the largest carnivores in New Mexico during the Barstovian.

Canidae

Borophaginae– Borophagines are common carnivores of the Tesuque fauna and often the most prevalent carnivorans. They are also taxonomically diverse members of the fauna. *Cynarctoides acridens* was first named from material collected from the late Oligocene-early Miocene of Nebraska by Barbour and Cook (1914), and its presence in the Nambé and Skull Ridge members was cited by Wang et al. (1999). Munthe (1998) noted the presence of an indeterminate species of *Cynarctus* in the Skull Ridge Member, although this specimen is now believed to represent *Cynarctoides acridens*. *Tephrocyon kelloggi* was named by Merriam (1911) from material from the middle Miocene of Nevada and was transferred to *Paracynarctus* by Wang et al. (1999). Munthe (1998) noted its presence in the Nambé Member, while Wang et al. (1999) cited *P. kelloggi* from both the Nambé and Skull Ridge members. *Tephrocyon confertus*, a small borophagine, was named by Matthew (1918) from material from the middle Miocene of Nebraska and was transferred to *Microtomarctus* by Wang et al. (1999). Munthe (1998) cited its presence in the Skull Ridge and Chama-El Rito members, while Wang et al. (1999) noted it from the Nambé, Skull Ridge, Pojoaque, and Chama-El Rito members. This potentially makes *Microtomarctus conferta* the longest ranging borophagine species in the Tesuque Formation. Additionally, Munthe (1998) noted the presence of *Tomarctus paulus* in the Pojoaque Member, although this taxon was considered a junior synonym of *M. conferta* by Wang et al. (1999). Munthe (1998) also noted the presence of *Tomarctus optatus*, originally identified by Matthew (1924) from material from the early Miocene of Nebraska, in the Nambé Member of the Tesuque Formation. However, Wang et al. (1999), who transferred the species to *Protomarctus*, did not list it in the Tesuque Formation. Other borophagine taxa noted from the Nambé Member (e.g., *Cynarctoides acridens*, *Microtomarctus conferta*,

TABLE 1. Fossil carnivorans present in the Tesuque Formation by member. Identifications from previous studies are discussed in the text. For how body size was used, see Methods section of text. **Abbreviations**: **x**, present in given member; *****, holotype specimen from given member.

Family	Subfamily	Genus/Species	Body Size	Nambé	Skull Ridge	Pojoaque	Chama-El Rito	Ojo Caliente
Amphicyonidae	Amphicyoninae	*Amphicyon ingens*	large			x		
Amphicyonidae	Amphicyoninae	*Pseudocyon* sp.	large			x		
Canidae	Borophaginae	*Aelurodon ferox*	large			x	x	x
Canidae	Borophaginae	*Aelurodon stirtoni*	large			x	x	
Canidae	Borophaginae	*Aelurodon taxoides*	large					
Canidae	Borophaginae	*Aelurodon* sp.	large		x	x		x
Canidae	Borophaginae	*Carpocyon webbi*	large			x		x
Canidae	Borophaginae	*Cynarctoides acridens*	small	x	x			
Canidae	Borophaginae	*Epicyon haydeni*	large			x	x	
Canidae	Borophaginae	*Epicyon saevus*	large			x		
Canidae	Borophaginae	*Microtomarctus conferta*	small	x	x	x	x	
Canidae	Borophaginae	*Paracynarctus kelloggi*	small	x	x			
Canidae	Borophaginae	*Paratomarctus temerarius*	small			x	x	x
Canidae	Borophaginae	*Psalidocyon marianae*	small		x*			
Canidae	Borophaginae	*Tomarctus brevirostris*	small		x			
Canidae	Borophaginae	*Tomarctus hippophaga*	small		x			
Canidae	Borophaginae	*Tomarctus* sp.	small			x	x	
Canidae	Caninae	*Leptocyon leidyi*	small		x			
Canidae	Caninae	*Leptocyon vafer*	small			x		x
Canidae	Hemicyoninae	*Plithocyon ursinus*	large			x*		
Mephitidae	Mephitinae	*Martinogale nambiana*	small			x		
Mephitidae	Mephitinae	*Martinogale* sp.	small			x		
Mustelidae	Mustelinae	*Mustela* sp.	small			x		
Mustelidae	Mustelinae	*Plionictis* sp.	small		x	x		
Mustelidae	Mustelinae	*Sthenictis* sp.	small			x	x	
Mustelidae	Oligobuninae	*Brachypsalis* sp.	large		x	x		
Mustelidae	*incertae sedis*	*Miomustela* sp.	small		x			
Procyonidae	Procyoninae	*Bassariscus* sp.	small		x	x		
Ursidae	Hesperocyoninae	*Osbornodon fricki*	large		x*			
Felidae	*incertae sedis*	*Pseudaelurus marshi*	small			x		
Felidae	*incertae sedis*	*Pseudaelurus stouti*	small		x	x		
Felidae	*incertae sedis*	*Pseudaelurus validus*	small	x*				
Felidae	*incertae sedis*	*Pseudaelurus* sp.	small		x	x		

and *Paracynarctus kelloggi*) have not had *P. optatus* specimens referred to them (Wang et al., 1999), and without further information the referral of the Nambé Member *P. optatus* specimens to any of these other taxa is uncertain. Nevertheless, it appears that *P. optatus* is not currently recognized from the Nambé Member or the Tesuque Formation, and no known Tesuque specimens are definitively referred to this taxon.

Psalidocyon marianae was named by Wang et al. (1999) from the Skull Ridge Member of the Tesuque Formation. It currently remains the only borophagine named from the Tesuque Formation, and the holotype is the only material of the taxon yet identified from New Mexico. *Psalidocyon marianae* also represents one of five carnivoran taxa named from the Tesuque Formation, and one of two from the Skull Ridge Member. *Tephrocyon hippophagus* was named by Matthew and Cook (1909) from material from the middle Miocene of Nebraska and was transferred to the genus *Tomarctus* by VanderHoof (1931) as *Tomarctus hippophaga*. *Tomarctus brevirostris* was named by Cope (1873) from material from Colorado and believed to be middle Miocene in age. Wang et al. (1999) cited both species from the Skull Ridge Member. Additionally, Munthe (1998) noted an indeterminate species of *Tomarctus* in the Chama-El Rito Member as well. Here I note the rare presence of *Tomarctus* in both the Pojoaque and Chama-El Rito members as well, although none are identified to species level. Still, this marks the first report of *Tomartcus* in the Pojoaque Member and shows that *Tomarctus* persisted at least into the Late Barstovian in New Mexico.

Strobodon stirtoni, a borophagine first known from the middle Miocene of Nebraska, was named by Webb (1969). It was later moved to the genus *Aelurodon* by Wang et al. (1999), who cited its occurrence in the Pojoaque and Chama-El Rito members of the Tesuque Formation. Munthe (1998) and Aby et al. (2011) noted its presence in the Pojoaque Member as well. *Aelurodon ferox* was named by Leidy (1858) from material collected from Nebraska and believed to be middle Miocene in age (VanderHoof and Gregory, 1940; Wang et al., 1999). Indeed, Wang et al. (1999) cited its occurrence in the Pojoaque, Chama-El Rito, and Ojo Caliente members, while Aby et al. (2011) noted its occurrence in the Pojoaque Member in their review of the paleontology of that member. *Aelurodon taxoides* was named by Hatcher (1893) from material from the middle Miocene of Nebraska. Wang et al. (1999) cited a single specimen from the Dixon Member of the Tesuque Formation, making it the only carnivoran specimen known from that member. Munthe (1998) noted the presence of *A. ferox* in the Pojoaque, Chama-El Rito, and Dixon members; *A. taxoides* in the Skull Ridge and Ojo Caliente members; and the presence of an indeterminate species of *Aelurodon* in the Chama-El Rito Member. However, based on the work of Wang et al. (1999) and the specimens themselves, it is believed that the *A. ferox* specimen from the Dixon Member is actually referable to *A. taxoides*; the *A. taxoides* specimens mentioned by Munthe (1998) are actually referable to *A. ferox*, and the indeterminate *Aelurodon* specimens are probably referable to *A. ferox*. In addition to the three species of *Aelurodon* noted above, the presence of this genus is noted from the Skull Ridge Member, making it a rare component in the Early Barstovian of New Mexico before it became more prevalent in the Late Barstovian in New Mexico.

Carpocyon webbi was named by Wang et al. (1999) from material from the middle Miocene of Nebraska and referred specimens to this taxon from the Pojoaque and Ojo Caliente members. This borophagine was also cited from the Pojoaque Member by Aby et al. (2011). Indeed, specimens referred to indeterminate species of *Carpocyon* were also noted by Munthe (1998) from the Pojoaque and Chama-El Rito members. However, no distinct specimens from the Chama-El Rito Member have been identified as *Carpocyon* that I am aware of in any of the collections investigated. Even so, this means that there remains a high probability of finding specimens referable to this taxon in the Chama-El Rito Member as well.

Both *Canis saevus* and *Canis* (*Epicyon*) *haydeni* were first named by Leidy (1858) from material from the middle Miocene of Nebraska, and both were definitively transferred to the genus *Epicyon* by Baskin (1980). Wang et al. (1999) maintained both as species of *Epicyon*, and while both *E. saevus* and *E. haydeni* were cited as present in the Pojoaque Member, they only cited the presence of *E. haydeni* in the Chama-El Rito Member. Indeed, Aby et al. (2011) only mentioned the presence of *E. saevus* when discussing the Pojoaque Member. Additionally, an indeterminate species of *Epicyon* was noted by Munthe (1998), which may refer to either of the above mentioned species. Finally, *Canis temerarius* was also named by Leidy (1858) from material (USNM 768, lectotype) from the middle Miocene of Nebraska and transferred to the distinct genus *Paratomarctus* by Wang et al. (1999). The latter authors also cited its occurrence in the Pojoaque, Chama-El Rito, and Ojo Caliente members of the Tesuque Formation. Additionally, it is noted that Aby et al. (2011) cited the occurrence of *Paratomarctus temerarius* in the Pojoaque Member as well.

Caninae– Canines represent small carnivores from the Tesuque fauna. The canine *Leptocyon leidyi* was named by Tedford et al. (2009) based on material from the early Miocene of Nebraska. It was originally referred to *L. vafer* by Matthew (1918). Tedford et al. (2009) identified *L. leidyi* from the early Barstovian Skull Ridge Member of the Tesuque Formation, and this occurrence is agreed on in the present study. *Canis vafer* was named by Leidy (1858) based on material from the late Barstovian of Nebraska and was later also transferred to *Leptocyon* by Matthew (1918). The presence of *Leptocyon vafer* in the Pojoaque Member was noted by Munthe (1998), Tedford et al. (2009), and Aby et al. (2011). Additionally, Tedford et al. (2009) noted its presence in the Ojo Caliente Member. It is identified here from the younger Pojoaque and Ojo Caliente members as well.

Hesperocyoninae– *Osbornodon* was named by Wang (1994) with *O. fricki* as the genotypic species. *Osbornodon fricki* was named by Wang (1994) from material from the early Barstovian Skull Ridge Member of the Tesuque Formation and represents one of only five carnivoran taxa with types from the Tesuque Formation and one of only two from the Skull Ridge Member. Its presence in the Skull Ridge Member was also mentioned by Munthe (1998). Not only does *O. fricki* represent a large hypercarnivore to mesocarnivore in the Tesuque fauna, but it also represents the last of the hesperocyonines (Wang, 1994; Munthe, 1998).

Ursidae

Hemicyoninae– The ursid *Plithocyon ursinus* has been identified from the Pojoaque Member of the Tesuque Formation (Cope, 1875; Hunt, 1998a; Aby et al., 2011). Indeed, the holotype (USNM 2040) from the Pojoaque Member was originally named *Canis ursinus* by Cope (1875), and its generic placement has shifted over time. It was moved to the amphicyonid genus *Amphicyon* by Cope (1879), questionably to the borophagine genus *Aelurodon* by Scott (1890), to the hemicyonid genus *Dinocyon* by Matthew (1902), to the hemicyonid genus *Hemicyon* by Frick (1926) and VanderHoof and Gregory (1940) and finally to the hemicyonine ursid genus *Plithocyon* by Hunt (1998a). While some studies place Hemicyonidae as its own family (e.g., McKenna and Bell, 1997), others place it as a subfamily in the Ursidae (e.g., Hunt, 1998a), with the classification of the latter followed herein. Note that in the present study it is maintained as a subfamily, in which case ursids (in the context of the present study) refer to all non-hemicyonine ursids. *Plithocyon ursinus* represents one of five carnivoran taxa named from holotype material from the Tesuque Formation, and one of two from the Pojoaque Member.

Mephitidae

Mephitinae– The phylogenetic position of skunks has often varied between the family and subfamily levels (see Wang et al., 2005, 2014; Wang and Carranza-Castañeda, 2008). Wang et al. (2005) placed the group as a subfamily within Musteloidea, while Wang and Carranza-Castañeda (2008) and Wang et al. (2014) considered Mephitidae its own family (see discussion within latter two studies). However, whether there were basal taxonomic members within the family that were outside the subfamily Mephitinae was not discussed or shown by either study.

Martes nambianus was named by Cope (1874) based on a partial lower jaw (USNM 1038) from the Santa Fe Marls and moved to the genus *Purtorius* by Cope (1877). Hall (1930) created the genus *Martinogale* and referred the species *Martes nambianus* (or *Purtorius nambianus*) to his genus. Baskin (1998b), on the other hand, noted that USNM 1038 (holotype of *Martes nambianus*) was from the Pojoaque Member and maintained the species within *Martinogale* (*M. nambiana*). However, Wang et al. (2005) felt that a close relationship between *Martinogale alveodens* and "*Martes*" *nambianus* could not be recognized based on the material available. They did not examine the type of *M. nambianus* directly, but still felt that it was unlikely that it was related to *Martinogale*. Aby et al. (2011), on the other hand, referred the species to *Pliogale*, creating *P. nambiana*. Even so, *Martinogale nambiana* is maintained here until further study shows its true generic affinities. *Martinogale* has been identified from the Tesuque Formation (and specifically the Pojoaque Member) by Cope (1874), Chaney (2009) and Aby et al. (2011), with others discussing *Martinogale nambiana*, and therefore its presence in the Tesuque Formation (e.g., Cope, 1874; Hall, 1930; Wang et al., 2005). Indeed, additional material identified as "*Martinogale* sp." is also known from the Pojoaque Member (e.g., Chaney, 2009), however it is probably referable to the genus to which *M. nambiana* is eventually assigned. Nevertheless, *Martinogale nambiana* represents one of five carnivoran taxa with holotype specimens from the Tesuque Formation, and one of two from the Pojoaque Member. Additionally, it is noted that *Martinogale*, as a basal skunk, may lie outside the Mephitinae as a basal member of the Mephitidae, however it is maintained here as a basal mephitine until further study is conducted.

Mustelidae

Various subfamilies– Depending on the systematic placement of Mephitinae, the specimens identified as such (including *Martinogale nambiana* and *Martinogale* sp.) may be included as mustelids. However, they are not included in Mustelidae in the present study (see discussion above). Other mustelid taxa have not been previously reported from the Tesuque Formation. However, several mustelid genera are reported here from the Tesuque Formation for the first time.

Brachypsalis was first identified from the Miocene of Nebraska by Cope (1890), and is identified here from the Skull Ridge and Pojoaque members. It was placed in the Oligobuninae by Baskin (1998b). *Miomustela* was first identified from the upper Miocene of Montana by Hall (1930), and is identified here from the Skull Ridge Member. While *Miomustela* was considered a member of the Mustelinae by McKenna and Bell (1997), Baskin (1998b) considered the genus in subfamily *incertae sedis*, and the latter study is conservatively followed here. *Mustela*, the modern genus, is also tentatively identified from the Pojoaque Member, however it is noted that the specimens identified as such probably represent another mustelid genus. *Plionictis* was first identified from the middle to late Miocene of Nebraska by Matthew (1924), and is identified here from the Skull Ridge and Pojoaque members. Finally, *Sthenictis* was first identified from the Miocene of Nebraska by Peterson (1910), and is identified here from the Pojoaque and Chama-El Rito members, potentially representing the youngest mustelid known from the Tesuque Formation. *Mustela*, *Plionictis*, and *Sthenicits* are all considered mustelines by McKenna and Bell (1997) and Baskin (1998b). However, because so few mustelid specimens are known from the Tesuque Formation, let alone from the individual subfamilies, they are grouped together in the Mustelidae for the statistical purposes of this study.

Procyonidae

Procyoninae– Procyonids make up a rare component of the Tesuque carnivoran fauna. Previous mentions of procyonids from the formation were by Chaney (2009) and Aby et al. (2011). Both these studies cited the occurrence of *Bassariscus* in the Pojoaque Member. While some studies consider *Bassariscus* a member of the subfamily Bassariscinae (e.g., McKenna and Bell, 1997), others consider it a member of the Procyoninae (e.g., Baskin, 1998a), and the latter assignment is used here. In the present study it is apparent that an indeterminate species of the procyonine *Bassariscus*, and procyonids in general, make up a small proportion of the Tesuque fauna. Additionally, I report the first occurrence of *Bassariscus* in the older Skull Ridge Member as well, albeit still as a rare component.

Feliformia
Felidae

Felidae *incertae sedis*– Felids make up a relatively small portion of the Tesuque fauna. Felids have been cited from the Tesuque Formation in several previous studies (Martin, 1998; Rothwell, 2001, 2003, Aby et al., 2011). The genus *Pseudaelurus* was first named from Europe by Gervais (1850), and eventually the cat *Felis intrepidus* (Leidy, 1858) was moved to this genus by Leidy (1869), marking the first known species of the genus in North America. See Rothwell (2003) for a thorough review of North American *Pseudaelurus*.

Pseudaelurus marshi was first named by Thorpe (1922) from material from the middle Miocene of Nebraska. *Lynx stouti* was originally named from material from the middle Miocene of Colorado by Schultz and Martin (1972), and was moved to *Pseudaelurus* as *P. stouti* by Rothwell (2003). Finally, Rothwell (2001) named *Pseudaelurus validus* from the Nambé Member of the Tesuque Formation. Additionally, in his review of *Pseudaelurus*, Rothwell (2003) cited the occurrences of *Pseudealurus stouti* from the Skull Ridge and Pojoaque members, and *P. marshi* from the Pojoaque Member. Moreover, Martin (1998) cited the presence of *P. marshi* from the Nambé Member, however this material is probably referable to *P. validus*, and *Pseudaelurus* from the Pojoaque Member, which is probably actually referable to *P. marshi* or *P. stouti*. Aby et al. (2011) mentioned the presence of *P. marshi* and *P. stouti* in the Pojoaque Member, without further comment. Additional specimens of *Pseudaelurus* have been identified from the Skull Ridge and Pojoaque members, although they have not been referred to *P. marshi* or *P. stouti* or another species. While previous studies have listed *Pseudaelurus* as a member of the Felinae (e.g., McKenna and Bell, 1997; Martin, 1998), more recent work considers it to be a basal felid and part of subfamily *incertae sedis* within Felidae (Rothwell, 2001, 2003), with the current study following the latter placement. Nevertheless, *Pseudaelurus validus* represents one of only five carnivoran taxa named from holotype material from the Tesuque Formation, and the only one from the Nambé Member.

PALEOECOLOGY

Relatively little has been published on the paleoecology and potential paleoenvironment of the Tesuque Formation and the middle Miocene of New Mexico and the American Southwest. In regards to the early Barstovian Skull Ridge Member, Axelrod and Bailey (1976) reported on a *Sabal* fossil palm (NMMNH P-56031) recovered from said member (also mentioned by Chaney, 2009). Based on its presence, the depositional environment of the Skull Ridge Member is estimated to have been approximately 700 meters above sea level with mild winters that would have been frost free or would have had frost occurring less than 0.5 hours per year and would have had approximately 212 days per year with an average mean temperature warmer than 15°C (Axelrod and Bailey, 1976).

Paleoenvironmental reconstructions of the late Barstovian Pojoaque Member have been mentioned in a few recent studies based on multiple localities (e.g., Chaney, 2009; Aby et al., 2011). Deposition of the Pojoaque Member would have taken place in a basin adjacent to highlands and mountains to the east (Chaney, 2009). Indeed, the occurrence of piñon and white pine cones, along with ochotonid remains, implies elevations of approximately 2500 m for the sediment source area to the east. Plant-fossil rich horizons have also been found in the Pojoaque Member (McKinney et al., 2006), some of which contain bristlecone pine and willow fossils among others (McKinney pers. comm., 2011 via Aby et al., 2011). Aby et al. (2011) noted that these fossils, particularly those of the bristlecone pine, indicated a colder, and potentially a "subalpine" climate. In particular, the Jacona Microfauna Quarry, which Chaney (2009) reported on, was believed to represent a pond environment. The study area of Aby et al. (2011) was believed to be near the confluence of a broad alluvial slope and a basin with highlands to the east and northeast and the Jemez Mountains volcanic field developing to the west (Kuhle and Smith, 2001; Smith, 2004). Over time the boundary between the alluvial slope and basin floor migrated back and forth across the study area of Aby et al. (2011).

Axelrod and Bailey (1976) noted that the warm climate of the Skull Ridge Member, suggested by the palm fossil, was in contrast to colder climates inferred from subalpine conifer forests present in older Oligocene strata near Hermosa and Hillsboro south of the outcrops of the Tesuque Formation in New Mexico. Axelrod and Bailey (1976), in estimating an elevation of approximately 700 m during the deposition of the Skull Ridge Member, found that the basin and study area would have risen by approximately 1200 m to get to its current elevation at over 1800 m. Indeed Meyer (1983), in reporting on the Socorro fossil flora from the Miocene Popotosa Formation (see Morgan et al., 2009), found a similar change in elevation from the time of deposition to the present day. Regardless, indications for both warmer and colder climates have been identified in the Tesuque Formation, leading to a diverse and changing climate and environment, and would have affected the paleoecology of the carnivorans present.

RESULTS

In order to view changes throughout the Tesuque Formation, carnivoran diversity through time was investigated. Diversity, based on number of carnivoran taxonomic groups, changes in the middle Miocene in the Tesuque Formation (Fig. 2). Diversity rises from the Nambé through the Pojoaque members, then drops drastically in the Chama-El Rito Member, and continues to drop, albeit at a much slower rate, through the Ojo Caliente and into the Dixon members. Separating the groups into their NISP to determine the percentages of each within each member provides further data (Fig. 3). Borophagines make up the majority of the fauna in each member, although in some members this percentage is lower. Canines are usually the second most abundant carnivoran in each member of the Tesuque Formation. Additionally, in the members where the percentage of borophagines drops, the percentage of canines rises. Indeed, the rise and fall of the percentages of borophagines and canines show inverse relationships (Fig. 3A).

As noted above, the Skull Ridge (early Barstovian) and Pojoaque (late Barstovian) faunas were the best sampled of the members of the Tesuque Formation. As such, comparisons of the carnivorans from these two members allows for more information dealing with the change in the carnivoran fauna of the Tesuque Formation during the Barstovian in New Mexico (Fig. 4). Borophagines make up the majority of the carnivoran fauna throughout the Barstovian, followed by canines. However, the faunal composition of the other carnivorans does change throughout the Barstovian and middle Miocene. During the early Barstovian, there are smaller percentages of mustelids, hesperocyonines, and felids, with procyonines being a rare component (Fig. 4A). However, in the late Barstovian the rare carnivorans are the mustelids and felids, with the rarest now being the amphicyonines, hemicyonines, mephitines, and procyonines (Fig. 4B).

Additionally, the middle Miocene carnivoran fauna of New Mexico (i.e., the Tesuque Formation) was compared to that of North America during the middle Miocene using data from the Paleobiology Database (www.fossilworks.org) (Fig. 5). As the Tesuque carnivorans were compared as a whole, the carnivoran faunal composition was generally different than those discussed for the individual members. Borophagines still make up the majority of the Tesuque carnivorans, and canines are still the second most prominent (Fig. 5A). After borophagines and canines, there are mustelids, felids, hesperocyonines, hemicyonines, mephitines, procyonines, and amphicyonines, in relative decreasing order of abundance. Indeed, including hesperocyonines, the guild of canids make up just over 85% of the Tesuque carnivoran population.

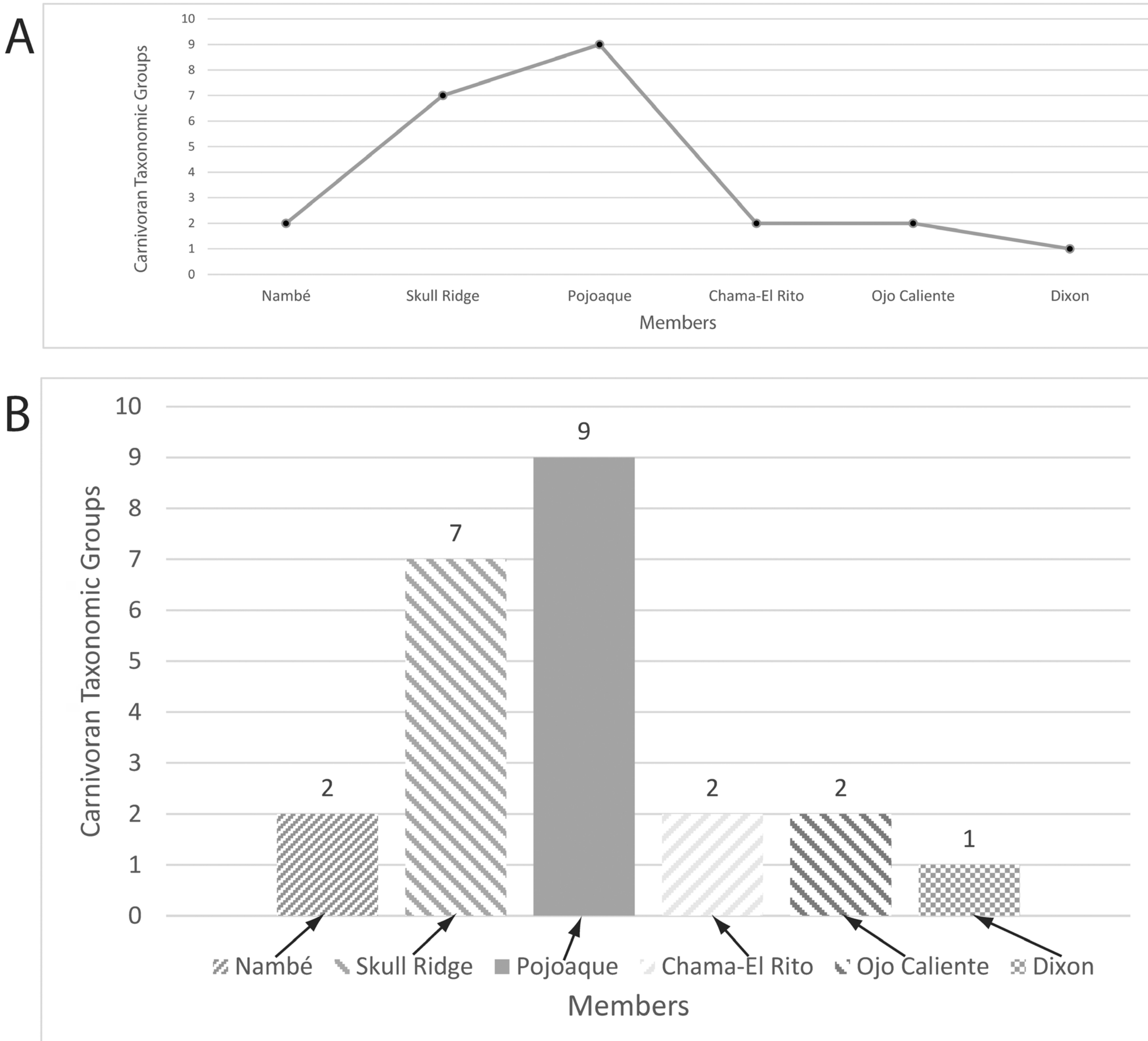

FIGURE 2. Plot of the number of taxonomic groups of Carnivora found in each member of the Tesuque Formation. (**A**), connected scatter plot and (**B**), bar graph.

When looking at the middle Miocene of North America as a whole, however, there is far more diversity (Figs. 5B and 5C). In comparing the terrestrial carnivores from the middle Miocene of North America to the carnivorans of New Mexico (Tesuque Formation), the only group represented in the former and not the latter are ursids (i.e., “non-hemicyonine ursids”). Borophagines still make up the majority of the carnivoran fauna (Fig. 5B). However, canines are not the second-most abundant carnivoran for all of North America, instead being third (mustelids are second). Amphicyonids, procyonids, and felids are somewhat rare, but more abundant than in the Tesuque Formation. It is noted that for some groups in North America, family-level classification was used. Whenever possible the same taxonomic level was used for comparison between the Tesuque Formation and North America as a whole, however that was not always possible with the information available. Nevertheless, comparisons can still be made, as some of the subfamilies used for New Mexico and the Tesuque Formation are equivalent to their higher-ranked families because they are represented by only a single subfamily (e.g., Amphicyoninae and Amphicyonidae, Hemicyoninae and Ursidae, Mustelinae and Mustelidae, Procyoninae and Procyonidae). It is noted that when looking at all carnivorans from North America (Fig. 5C), the main additions in particular are several aquatic and marine carnivorans (e.g., Desmatophocidae, Odobenidae, Otariidae, Phocidae). Relationships between the carnivorans present in both groups (Figs. 5A and 5C) are similar to those between the terrestrial carnivorans (Figs. 5A and 5B) except that the percentages of the similar groups are lower in Figure 5C compared to Figure 5B. Even so, comparisons between New Mexico and North America as a whole remain similar.

The rarefaction curves for members with NISP ≥10 carnivoran specimens and for the Tesuque Formation as a whole were derived (Fig. 6). For the majority of the members, taxonomic diversity is greater in members with more fossil carnivoran specimens known, although the curve for the Ojo Caliente Member is steeper than that of the Chama-El Rito Member, even though the former has less known carnivoran specimens than the latter. Nevertheless, for the majority of the members, more specimens translates to more taxonomic diversity, with the Tesuque Formation as a whole showing the most taxonomic diversity and the steepest rarefaction curve.

The cluster analysis examining taxonomic groups shows two distinct clusters (Fig. 7). One cluster is made up of ((Felidae, Mustelidae, Caninae, Procyoninae), Borophaginae) and the other of (Amphicyoninae, Hemicyoninae, Mephitinae), with Hesperocyoninae falling outside of both. This relationship may be due to the fact that Hesperocyoninae is only present in a single member. Although it is noted that amphicyonines are also only present in one member, they still group with hemicyonines and mephitines. Borophaginae clustering

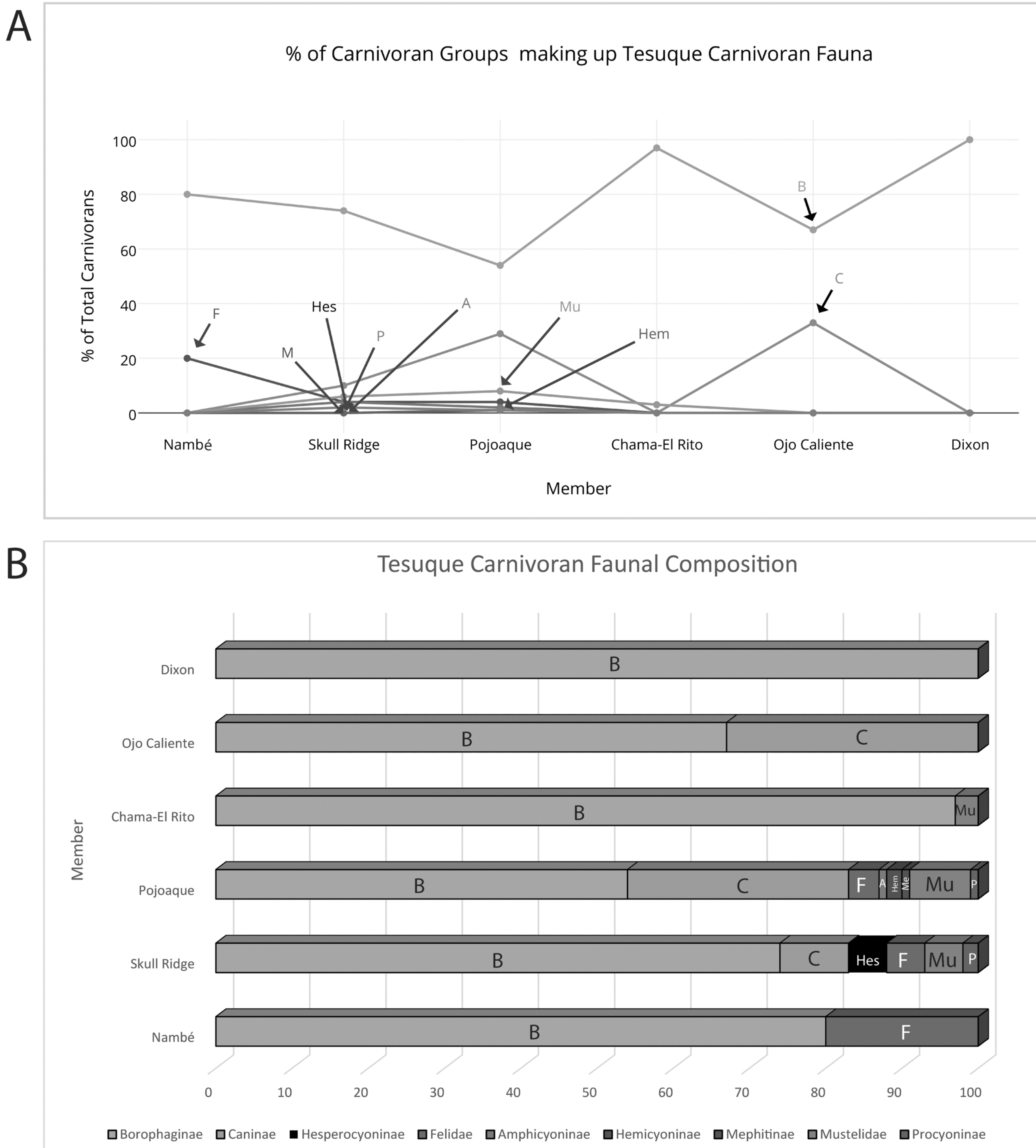

FIGURE 3. Percentage of each carnivoran taxonomic group present within each member of the Tesuque Formation. Note the inverse relationship between Borophaginae and Caninae, the drop in the abundance of Felidae through time, and the low abundances of the other groups in relation to Borophaginae and Caninae. (**A**), connected scatter plot and (**B**), bar graph. **Abbreviations**: **A**, Amphicyoninae; **B**, Borophaginae; **C**, Caninae; **F**, Felidae; **Hem**, Hemicyoninae; **Hes**, Hesperocyoninae; **Me**, Mephitinae; **Mu**, Mustelidae; **P**, Procyoninae.

just outside the Felidae, Caninae, Mustelidae, and Procyoninae groups suggests that it shares multiple sites with the others. Similarity indices for the ((Felidae, Mustelidae, Caninae, Procyoninae), Borophaginae) cluster support that while the distribution of these groups within each member are similar, they vary just enough for a weaker index value (J(Felidae, Mustelidae, Caninae, Procyoninae)=0.47; (J(Felidae, Mustelidae, Caninae, Procyoninae), Borophaginae)=0.4). The similarity index for the (Amphicyoninae, Hemicyoninae, Mephitinae) strongly supports these taxonomic groups being similar in their distribution among the Tesuque members (J(Amphicyoninae, Hemicyoninae, Mephitinae)=0.0).

The cluster analysis of the members of the Tesuque Formation grouped the Skull Ridge and Pojoaque as the only two members that were distinct (Fig. 8). This relationship was further supported by the Bray-Curtis coefficient between these two members (S=0.462, see Table 2). However, the Raup-Crick probability was not statistically significant (p=0.667, see Table 2). This suggests that while there is statistical support for the similarity between the two members, it is not

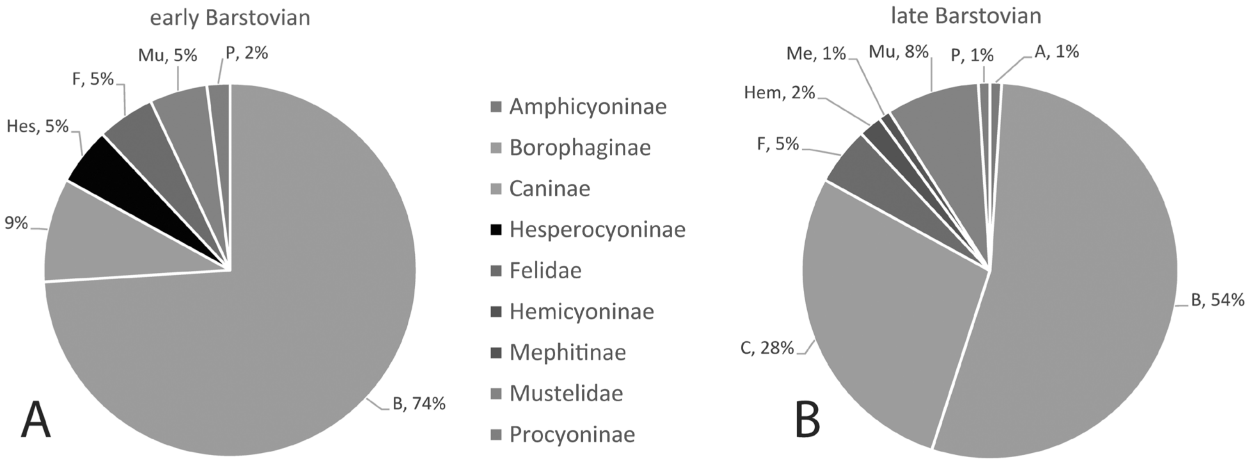

FIGURE 4. Pie charts showing the carnivoran faunal composition and percentages during the Barstovian (middle Miocene) of New Mexico based on fossil carnivorans from the Tesuque Formation. (**A**), early Barstovian and (**B**), late Barstovian of the Tesuque Formation in New Mexico. **Abbreviations**: **A**, Amphicyoninae; **B**, Borophaginae; **C**, Caninae; **F**, Felidae; **Hem**, Hemicyoninae; **Hes**, Hesperocyoninae; **Me**, Mephitinae; **Mu**, Mustelidae; **P**, Procyoninae.

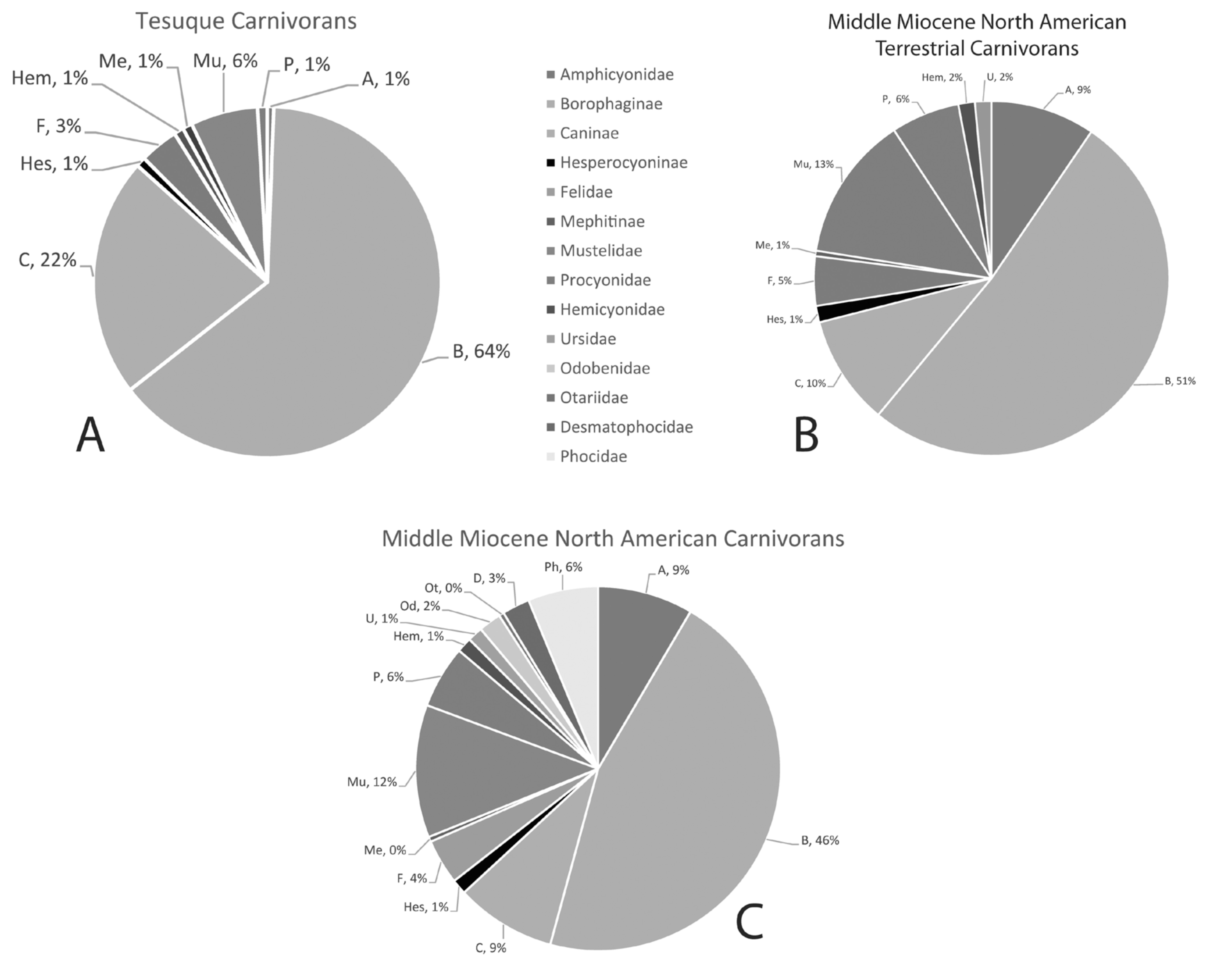

FIGURE 5. Pie charts showing the carnivoran faunal composition and percentages during the middle Miocene of New Mexico (Tesuque Formation) and North American formations as a whole. (**A**), fossil carnivorans from the middle Miocene Tesuque Formation of New Mexico, (**B**), terrestrial fossil carnivorans from the middle Miocene of North America, and (**C**), all fossil carnivorans from the middle Miocene of North America. **Abbreviations**, **A**, Amphicyoninae; **B**, Borophaginae; **C**, Caninae; **D**, Desmatophocidae; **F**, Felidae; **Hem**, Hemicyoninae (Hemicyonidae); **Hes**, Hesperocyoninae; **Me**, Mephitinae; **Mu**, Mustelidae; **Od**, Odobenidae; **Ot**, Otariidae; **P**, Procyoninae (Procyonidae); **Ph**, Phocidae; **U**, Ursidae. Note that Hemicyoninae in (**A**) and Hemicyonidae in (**B** and **C**) are equivalent groups, just placed at different levels. Also note that Hemicyonidae is considered a subfamily in the present study, which means that the Ursidae in (**B** and **C**) refers to non-hemicyonine ursids. Note that and Procyoninae in (**A**) and Procyonidae in (**B** and **C**) are equivalent groups as well, just placed at different levels. Also note that although the percentages for Mephitinae and Otariidae are listed as “0%”, their percentages are actually less than 1% (=0.44%). See text for further discussion.

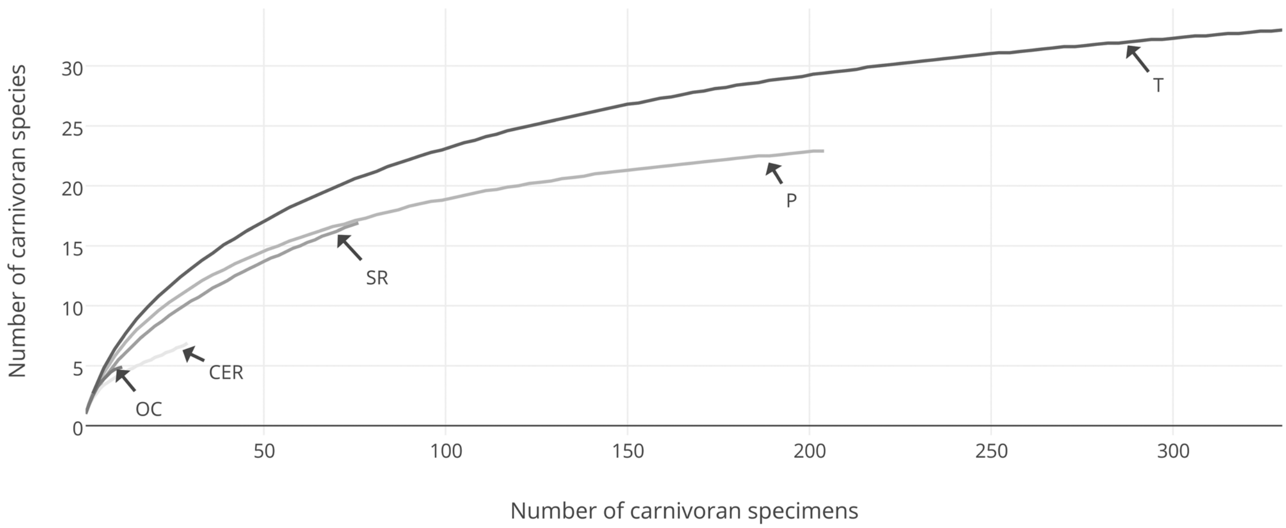

FIGURE 6. Rarefaction curves of fossil carnivorans from the middle Miocene Tesuque Formation of New Mexico. **Abbreviations**, **CER**, Chama-El Rito Member; **OC**, Ojo Caliente Member; **P**, Pojoaque Member; **SR**, Skull Ridge Member; **T**, Tesuque Formation (as a whole).

greater than what would be expected at random given the current data.

DISCUSSION

The results show several interesting patterns, many of which become more apparent when looking at diversity and changes in and among the carnivoran taxonomic groups through time. Diversity itself tends to rise until the late Barstovian (Pojoaque Member), falling quickly thereafter (Fig. 2). While the faunal composition changes throughout, borophagines remain the most numerous carnivorans throughout the Tesuque Formation and make up the majority of the carnivorans (Fig. 3). Borophagines being the most prevalent carnivoran group present during this time has been noted by other authors as well (e.g., Wang et al., 1999). However, it is noted that their majority percentage drops significantly in the late Barstovian (Pojoaque) and Clarendonian (Ojo Caliente), while the percentage of canines rises at a similar (but inverse) rate. This inverse relationship between the borophagines and canines may mean that canines are filling some of the open niche space left by borophagines, or a subset thereof, and vice versa. When one group, in this instance borophagines, becomes less abundant and less diverse, canines become more abundant, potentially filling niches left open by borophagines. Inversely, when canines become less abundant, borophagines become more, potentially refilling these now open niches. It could also be that as borophagines grow in abundance they may take back niches from canines, thus causing canines to decrease in abundance. Regardless of the exact mechanism causing this, the inverse relationship appears to be real and not just an artifact of the data. While Tedford et al. (2009) discussed the rise of mesocarnivorous small canines like *Leptocyon* during the early Miocene coinciding with the general and slight fall of borophagines during this time, the inverse relationship presented herein has not been stated before.

TABLE 2. Raup-Crick and Bray-Curtis coefficients for adjacent members of the Tesuque Formation.

Member Comparison	**Raup-Crick ($p<0.05$)**	**Bray-Curtis coefficient**
Nambé to Skull Ridge	0.417	0.878
Skull Ridge to Pojoaque	0.667	0.462
Pojoaque to Chama-El Rito	0.778	0.729
Chama-El Rito to Ojo Caliente	0.389	0.667
Nambé to Ojo Caliente	0.389	0.5

Indeed, Figure 4 helps portray the differences seen between the carnivoran compositions even more clearly for the early and late Barstovian compared to Figure 3. While borophagines still make up the majority, it is clear that canines make up a larger percentage during the late Barstovian, even though the total percentage of borophagines

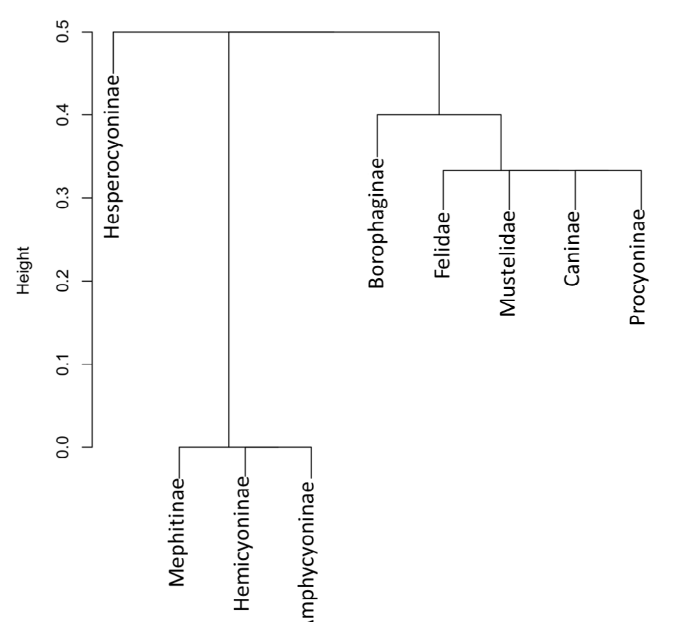

FIGURE 7. Single linkage cluster analysis of carnivoran taxonomic groups. Height indicates the similarity coefficient at a given node. Hesperocyoninae is represented by only a few specimens, possibly explaining its isolation from the other clusters.

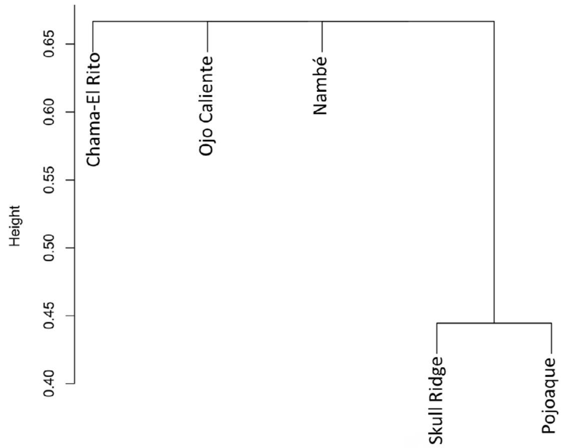

FIGURE 8. Cluster analysis of Tesuque Formation, with the Skull Ridge and Pojoaque members being the most similar in carnivoran faunas. This relationship is further supported by these members dating to the Barstovian North American land mammal age, and thus it would be expected for them to have similar carnivoran faunas.

and canines is nearly the same. Felids, as small hypercarnivores seem to maintain that niche throughout the Barstovian. As hesperocyonines seem to disappear as large predators in the Tesuque fauna after the early Barstovian, amphicyonines appear in the late Barstovian, perhaps helping to fill a large predatory niche.

While it is clear in Figure 5 that there is more overall carnivoran diversity known from the middle Miocene of North America than from the Tesuque Formation, a few points still stand out. These include the fact that canids (Borophaginae, Caninae, and Hesperocyoninae) make up a larger proportion of the carnivorans in New Mexico compared with the rest of North America. Mustelids and procyonids (or procyonines) on the other hand, make up a smaller proportion. It is also of note that the hypercarnivorous felids seem to make up similar proportions in both. New Mexico offers a near complete sampling of the terrestrial carnivoran families and groups present in the rest of North America during the middle Miocene as well.

The rarefaction curves derived for the Tesuque Formation tend to follow the trend of more carnivoran specimens leading to more taxonomic diversity and steeper rarefaction curves (Fig. 6). While the Ojo Caliente Member produces a steeper curve than that of the Chama-El Rito Member, both members have relatively lower numbers of carnivoran specimens, and the relationship between their diversities may be an artifact of that. Larger sample sizes will almost certainly lead to different curves and different relationships. The curvature of the rarefaction curve of the early Barstovian Skull Ridge Formation may imply that the carnivoran taxonomic diversity of this member would be higher than that of the late Barstovian Pojoaque Member if the sample size of the former was larger and more similar to that of the latter. As would be expected, the taxonomic diversity of the Tesuque Formation as a whole is more diverse than any of the individual members.

The cluster analysis of the carnivoran groups provides a sister relationship between borophagines and a cluster consisting of felids, mustelids, canines, and procyonines (Fig. 7). Indeed, when compared to the raw data, this relationship makes sense as Borophaginae is present in every member of the Tesuque Formation while the other groups may be found in only a few. Moreover, raw counts of each carnivoran taxonomic group when plotted against members show consistency in the presence of some groups while others fluctuate over time (Figs. 2 and 3). The strong similarity between the Amphicyoninae, Hemicyoninae, and Mephitinae cluster is due to all three subfamilies being represented by only a few specimens and their location in the same two members, the Pojoaque and Skull Ridge. Additional specimens within these subfamilies could support or refute this relationship as they are represented by such small counts.

As was noted above, the cluster analysis comparing the members of the Tesuque Formation provided little difference (Fig. 8). The Nambé, Chama-El Rito, and Ojo Caliente members came out at similar positions. The Skull Ridge and Pojoaque members group together as being distinct from the other members. This relationship was further supported by the Bray-Curtis coefficient between these two members. However, the Raup-Crick probability was not statistically significant.

In regards to the paleoecology of the carnivorans present, more work needs to be done to investigate the paleoenvironments present throughout the Tesuque Formation and the middle Miocene of New Mexico. Aby et al. (2011) noted the climate during the deposition of the Tesuque Formation would have then varied between warmer and potentially frost-free climates during the early Barstovian (*Sabal* palm fossil) to colder and potentially subalpine climates during the late Barstovian (bristlecone pine). However, they also noted that these differences may also have been from different areas of the basin or region. Indeed, with the boundaries between the highlands, alluvial slope, and basin floor migrating over time, and presumably throughout the middle Miocene, there may have been a shift in the depositional environment or a shift in the climate at the time of deposition. The majority of the carnivoran taxa discussed would have been able to survive in either of these climates, and those climates in between. Indeed, none of the taxa discussed are specifically adapted for incredibly cold or incredibly warm climates. However, as most of these fossils represent extinct taxa, understanding the climate throughout the Tesuque's deposition would allow more precise data on the paleoecology present during the middle Miocene of New Mexico as well. In addition to more information for the Skull Ridge and Pojoaque Members, additional data gathered from the other members of the Tesuque Formation would be quite valuable as well. Indeed, trends and patterns seen in the carnivoran fauna will have new and different interpretations when taken with more information on the paleoecology and paleoclimate of the middle Miocene of New Mexico during the deposition of the Tesuque Formation.

SUMMARY/CONCLUSIONS

The carnivoran fauna is dynamic during the middle Miocene (mainly Barstovian) of New Mexico when investigating the Tesuque Formation. Compiling the number of carnivorans and carnivoran species within each carnivoran taxonomic group in each member allows trends to emerge in appearances and extinctions over time and allows for better understanding of the changes in the carnivoran guilds of the middle Miocene carnivorans in New Mexico over time. In particular, borophagines are the most abundant carnivorans in the middle Miocene and the Barstovian of New Mexico. However, when borophagines become less abundant, canines grow in abundance. Indeed they seem to have a somewhat inverse relationship when dealing with abundances, which may imply that some species within these groups were utilizing similar niches and competing for resources. This inverse relationship has not been shown before and may be due, in part, to borophagines showing a general downward trend and allowing canines to fill open niches and grow in general abundance. The Skull Ridge and Pojoaque members are the most similar in their carnivoran diversity. This is consistent with both members being within the Barstovian North American land mammal age. It may also be due to both members being more completely sampled, as some of the more poorly sampled and fossiliferous units (or members) may be underrepresented in their true carnivoran diversity. In comparing the middle Miocene carnivoran fauna of New Mexico to the rest of North America, the latter is more diverse, although this is not surprising given the greater range of habitat possibilities and the larger overall area. However, New Mexico contains a higher percentage of canids and a lower percentage of mustelids and procyonids. In addition, this study reports the first occurrence of the borophagine *Tomarctus* from the Pojoaque Member, of the borophagine *Aelurodon* from the Skull Ridge Member, of procyonids (the procyonine *Bassariscus*) from the Skull Ridge Member, and mustelids ("non-mephitine mustelids") from the Tesuque Formation, including; the mustelid *Miomustela* from the Skull Ridge Member, the musteline *Mustela* from the Pojoaque Member, the musteline *Plionictis* from the Skull Ridge and Pojoaque members, the musteline *Sthenictis* from the Pojoaque and Chama-El Rito members, and the oligobunine *Brachypsalis* from the Skull Ridge and Pojoaque members.

Rarefaction curves show generally more taxonomic diversity in members with larger numbers of carnivoran specimens. While the late Barstovian Pojoaque Member shows more taxonomic diversity than the early Barstovian Skull Ridge Member, the curvature of the latter suggests that it may exhibit higher diversity if its sample size was as large as the former. Nevertheless, the diversity of carnivorans is highest in the Tesuque Formation as a whole.

A cluster analysis performed on the carnivoran taxonomic groups finds that most of the groups cluster together since each is found in the majority of the members of the Tesuque Formation. The Hesperocyoninae are found to be distinct from the other groups in the Tesuque Formation, and part of the reason for this may be that the Hesperocyoninae are a rare part of the carnivoran fauna and are restricted to only one member, the Skull Ridge Member. Indeed, while similarities are present in carnivoran faunas between members, they are not greater than what could be expected to occur at random.

Climate varied during the deposition of the Tesuque Formation and during the middle Miocene of New Mexico. However more data and information are needed from the individual members of the formation, and in particular those that have not been studied as thoroughly as the Pojoaque (and the Skull Ridge), in order to better understand the paleoecology of the carnivorans present, and how climate may be affecting the carnivoran faunal dynamics. In regard to the fossil carnivorans, this study may be detecting a sampling and size bias in the data, particularly since Borophaginae and Caninae are so well represented. Other than the study and work by Chaney (2009), practically no work has been done for the collection and study of microverterbates in the Tesuque Formation. This may also be acting against the quantity of small carnivore fossils (e.g. felids, mephitines, mustelids, and procyonids) as well. This work suggests that future digs and collecting efforts within the Tesuque Formation may benefit from screen washing techniques and methods investigating microfossils to determine whether more small carnivorans were present.

The middle Miocene of New Mexico was a dynamic time in the evolution of Carnivora in North America. Patterns of species, richness of the carnivoran fauna, and examination of faunal turnover are all shown to be dynamic during this time and in this region. The similarities seen between New Mexico and the rest of North America during this time may partially be due to the Tesuque Formation being one of the best sampled middle Miocene units in North America, leading to its prominence for the continent's data. More data and fossils are needed from other middle Miocene units in North America for further comparisons to be made.

ACKNOWLEDGMENTS

I thank Leigha M. King (Oklahoma State University, Tulsa, Oklahoma) for helping get this projected started, help with the cluster analyses, and for reviewing an earlier version of the manuscript. Other members of the Oklahoma State University Center for Health Studies Vertebrate Paleontology Group, including faculty and students (including Paul Gignac, Anne Weil, Kent Smith, and Ian Browne, among others), and Haley O'Brien (Ohio University, Athens) provided helpful discussions and aided with some of the statistical analyses. Thanks are extended to Gary Morgan (New Mexico Museum of Natural History and Science, Albuquerque, New Mexico), Scott Aby (Muddy Springs Geology, Dixon, New Mexico), Steven Wallace (East Tennessee State University, Johnson City, Tennessee), and Xiaoming Wang (Los Angeles County Museum of Natural History, Los Angeles, California) for help with some references and relevant geology. Peter Dodson (University of Pennsylvania, Philadelphia, Pennsylvania) reviewed an earlier version of this manuscript. Gary Morgan, Scott Aby and Spencer Lucas (New Mexico Museum of Natural History and Science, Albuquerque, New Mexico) provided helpful reviews.

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APPENDIX

Fossil specimens utilized in the present study. Fossils are all from the Tesuque Formation of New Mexico. Specimens are grouped taxonomically within members. Current identifications are as accurate as warranted. Type specimens are bolded. Further information as to previous studies discussing any of the specimens within are discussed in the text. Institutional abbreviations: **AMNH**, American Museum of Natural History; **F:AM**, Frick Collection, American Museum of Natural History; **NMMNH**, New Mexico Museum of Natural History and Science; **USNM**, United States National Museum of Natural History. Abbreviations: **indet.**, indeterminate; **sp.**, species (as in indeterminate species of).

Member	Current Number	Family	Subfamily	Genus	Species	Type Status
Nambé						
	F:AM 63144	Canidae	Borophaginae	*Cynarctoides*	*acridens*	
	F:AM 105257	Canidae	Borophaginae	*Microtomarctus*	*conferta*	
	F:AM 67373	Canidae	Borophaginae	*Microtomarctus*	*conferta*	
	F:AM 50140	Canidae	Borophaginae	*Paracynarctus*	*kelloggi*	
	F:AM 62128	**Felidae**	***incertae sedis***	***Pseudaelurus***	***validus***	**Holotype**
Skull Ridge						
	F:AM 107703	Canidae	Borophaginae	*Aelurodon*	sp.	
	F:AM 49201	Canidae	Borophaginae	*Cynarctoides*	*acridens*	
	F:AM 63138	Canidae	Borophaginae	*Cynarctoides*	*acridens*	
	F:AM 144238	Canidae	Borophaginae	*Microtomarctus*	*conferta*	
	F:AM 27383B	Canidae	Borophaginae	*Microtomarctus*	*conferta*	
	F:AM 27391	Canidae	Borophaginae	*Microtomarctus*	*conferta*	
	F:AM 27391A	Canidae	Borophaginae	*Microtomarctus*	*conferta*	
	F:AM 27396A	Canidae	Borophaginae	*Microtomarctus*	*conferta*	
	F:AM 27396B	Canidae	Borophaginae	*Microtomarctus*	*conferta*	
	F:AM 27396C	Canidae	Borophaginae	*Microtomarctus*	*conferta*	
	F:AM 27396D	Canidae	Borophaginae	*Microtomarctus*	*conferta*	
	F:AM 27398Z	Canidae	Borophaginae	*Microtomarctus*	*conferta*	
	F:AM 27473	Canidae	Borophaginae	*Microtomarctus*	*conferta*	
	F:AM 27478	Canidae	Borophaginae	*Microtomarctus*	*conferta*	
	F:AM 50164	Canidae	Borophaginae	*Microtomarctus*	*conferta*	
	F:AM 50165	Canidae	Borophaginae	*Microtomarctus*	*conferta*	
	F:AM 50166	Canidae	Borophaginae	*Microtomarctus*	*conferta*	
	F:AM 50167	Canidae	Borophaginae	*Microtomarctus*	*conferta*	
	F:AM 50168	Canidae	Borophaginae	*Microtomarctus*	*conferta*	
	F:AM 50169	Canidae	Borophaginae	*Microtomarctus*	*conferta*	
	F:AM 50170	Canidae	Borophaginae	*Microtomarctus*	*conferta*	
	F:AM 50171	Canidae	Borophaginae	*Microtomarctus*	*conferta*	
	F:AM 50172	Canidae	Borophaginae	*Microtomarctus*	*conferta*	
	F:AM 50173	Canidae	Borophaginae	*Microtomarctus*	*conferta*	
	F:AM 50174	Canidae	Borophaginae	*Microtomarctus*	*conferta*	
	F:AM 50175	Canidae	Borophaginae	*Microtomarctus*	*conferta*	
	F:AM 50176	Canidae	Borophaginae	*Microtomarctus*	*conferta*	
	F:AM 50177Y	Canidae	Borophaginae	*Microtomarctus*	*conferta*	
	F:AM 50178	Canidae	Borophaginae	*Microtomarctus*	*conferta*	
	F:AM 50179	Canidae	Borophaginae	*Microtomarctus*	*conferta*	
	F:AM 50180	Canidae	Borophaginae	*Microtomarctus*	*conferta*	
	F:AM 50182	Canidae	Borophaginae	*Microtomarctus*	*conferta*	
	F:AM 50188	Canidae	Borophaginae	*Microtomarctus*	*conferta*	
	F:AM 67336	Canidae	Borophaginae	*Microtomarctus*	*conferta*	
	F:AM 67337	Canidae	Borophaginae	*Microtomarctus*	*conferta*	
	F:AM 67338	Canidae	Borophaginae	*Microtomarctus*	*conferta*	
	F:AM 105097	Canidae	Borophaginae	*Paracynarctus*	*kelloggi*	
	F:AM 27394	Canidae	Borophaginae	*Paracynarctus*	*kelloggi*	
	F:AM 27396	Canidae	Borophaginae	*Paracynarctus*	*kelloggi*	
	F:AM 27399	Canidae	Borophaginae	*Paracynarctus*	*kelloggi*	
	F:AM 27487	Canidae	Borophaginae	*Paracynarctus*	*kelloggi*	
	F:AM 27488	Canidae	Borophaginae	*Paracynarctus*	*kelloggi*	
	F:AM 50135	Canidae	Borophaginae	*Paracynarctus*	*kelloggi*	
	F:AM 50136	Canidae	Borophaginae	*Paracynarctus*	*kelloggi*	
	F:AM 50137	Canidae	Borophaginae	*Paracynarctus*	*kelloggi*	
	F:AM 50187	Canidae	Borophaginae	*Paracynarctus*	*kelloggi*	
	F:AM 27397	**Canidae**	**Borophaginae**	***Psalidocyon***	***marianae***	**Holotype**
	F:AM 27368	Canidae	Borophaginae	*Tomarctus*	*brevirostris*	
	F:AM 61182	Canidae	Borophaginae	*Tomarctus*	*brevirostris*	
	F:AM 27379	Canidae	Borophaginae	*Tomarctus*	*hippophaga*	
	F:AM 27381	Canidae	Borophaginae	*Tomarctus*	*hippophaga*	
	F:AM 27382	Canidae	Borophaginae	*Tomarctus*	*hippophaga*	
	F:AM 27383	Canidae	Borophaginae	*Tomarctus*	*hippophaga*	
	F:AM 27383A	Canidae	Borophaginae	*Tomarctus*	*hippophaga*	
	F:AM 27384	Canidae	Borophaginae	*Tomarctus*	*hippophaga*	
	F:AM 27470	Canidae	Borophaginae	*Tomarctus*	*hippophaga*	
	F:AM 50154	Canidae	Borophaginae	*Tomarctus*	*hippophaga*	
	F:AM 67899	Canidae	Borophaginae	*Tomarctus*	sp.	
	F:AM 27273	Canidae	Caninae	*Leptocyon*	*leidyi*	

	F:AM 50162	Canidae	Caninae	*Leptocyon*	*leidyi*	
	F:AM 50177	Canidae	Caninae	*Leptocyon*	*leidyi*	
	F:AM 63134	Canidae	Caninae	*Leptocyon*	*leidyi*	
	F:AM 63135	Canidae	Caninae	*Leptocyon*	*leidyi*	
	F:AM 67891	Canidae	Caninae	*Leptocyon*	*leidyi*	
	F:AM 67891A	Canidae	Caninae	*Leptocyon*	*leidyi*	
	F:AM 27361	Canidae	Hesperocyoninae	*Osbornodon*	*fricki*	
	F:AM 27363	**Canidae**	**Hesperocyoninae**	***Osbornodon***	***fricki***	**Holotype**
	F:AM 67116	Canidae	Hesperocyoninae	*Osbornodon*	*fricki*	
	NMMNH P-25129	Canidae	indeterminate	Canidae indet.		
	AMNH 140228	Felidae	*incertae sedis*	*Pseudaelurus*	*stouti*	
	F:AM 61931	Felidae	*incertae sedis*	*Pseudaelurus*	*stouti*	
	F:AM 62182	Felidae	*incertae sedis*	*Pseudaelurus*	sp.	
	F:AM 27460	Mustelidae	*incertae sedis*	*Brachypsalis*	sp.	
	F:AM 27445	Mustelidae	Mustelinae	*Miomustela*	sp.	
	F:AM 27435A	Mustelidae	Mustelinae	*Plionictis*	sp.	
	F:AM 49224	Mustelidae	Mustelinae	*Plionictis*	sp.	
	F:AM 27467	Procyonidae	Procyoninae	*Bassariscus*	sp.	
	NMMNH P-25133	indeterminate	indeterminate	Carnivora indet.		
Pojoaque						
	F:AM 49244	Amphicyonidae	Amphicyoninae	*Amphicyon*	*ingens*	
	F:AM 49247	Amphicyonidae	Amphicyoninae	*Pseudocyon*	sp.	
	AMNH 8309	Canidae	Borophaginae	*Aelurodon*	*ferox*	
	F:AM 107705	Canidae	Borophaginae	*Aelurodon*	*ferox*	
	F:AM 107706	Canidae	Borophaginae	*Aelurodon*	*ferox*	
	F:AM 107707	Canidae	Borophaginae	*Aelurodon*	*ferox*	
	F:AM 107708	Canidae	Borophaginae	*Aelurodon*	*ferox*	
	F:AM 27340A	Canidae	Borophaginae	*Aelurodon*	*ferox*	
	F:AM 27341	Canidae	Borophaginae	*Aelurodon*	*ferox*	
	F:AM 27343	Canidae	Borophaginae	*Aelurodon*	*ferox*	
	F:AM 27345	Canidae	Borophaginae	*Aelurodon*	*ferox*	
	F:AM 27346	Canidae	Borophaginae	*Aelurodon*	*ferox*	
	F:AM 27347	Canidae	Borophaginae	*Aelurodon*	*ferox*	
	F:AM 27349	Canidae	Borophaginae	*Aelurodon*	*ferox*	
	F:AM 27350	Canidae	Borophaginae	*Aelurodon*	*ferox*	
	F:AM 27351	Canidae	Borophaginae	*Aelurodon*	*ferox*	
	F:AM 27351A	Canidae	Borophaginae	*Aelurodon*	*ferox*	
	F:AM 27351B	Canidae	Borophaginae	*Aelurodon*	*ferox*	
	F:AM 27351C	Canidae	Borophaginae	*Aelurodon*	*ferox*	
	F:AM 27356	Canidae	Borophaginae	*Aelurodon*	*ferox*	
	F:AM 27357	Canidae	Borophaginae	*Aelurodon*	*ferox*	
	F:AM 27358	Canidae	Borophaginae	*Aelurodon*	*ferox*	
	F:AM 27360	Canidae	Borophaginae	*Aelurodon*	*ferox*	
	F:AM 27479	Canidae	Borophaginae	*Aelurodon*	*ferox*	
	F:AM 27490	Canidae	Borophaginae	*Aelurodon*	*ferox*	
	F:AM 27491	Canidae	Borophaginae	*Aelurodon*	*ferox*	
	F:AM 61721	Canidae	Borophaginae	*Aelurodon*	*ferox*	
	F:AM 61722	Canidae	Borophaginae	*Aelurodon*	*ferox*	
	F:AM 61723	Canidae	Borophaginae	*Aelurodon*	*ferox*	
	F:AM 61724	Canidae	Borophaginae	*Aelurodon*	*ferox*	
	F:AM 61729	Canidae	Borophaginae	*Aelurodon*	*ferox*	
	F:AM 61730	Canidae	Borophaginae	*Aelurodon*	*ferox*	
	F:AM 61733	Canidae	Borophaginae	*Aelurodon*	*ferox*	
	F:AM 61734	Canidae	Borophaginae	*Aelurodon*	*ferox*	
	F:AM 61736	Canidae	Borophaginae	*Aelurodon*	*ferox*	
	NMMNH P-57620	Canidae	Borophaginae	*Aelurodon*	*ferox*	
	NMMNH P-63412	Canidae	Borophaginae	*Aelurodon*	*ferox*	
	F:AM 27367	Canidae	Borophaginae	*Aelurodon*	*stirtoni*	
	F:AM 27474	Canidae	Borophaginae	*Aelurodon*	*stirtoni*	
	F:AM 27481	Canidae	Borophaginae	*Aelurodon*	*stirtoni*	
	F:AM 27492	Canidae	Borophaginae	*Aelurodon*	*stirtoni*	
	F:AM 70501	Canidae	Borophaginae	*Aelurodon*	*stirtoni*	
	F:AM 8309	Canidae	Borophaginae	*Aelurodon*	*stirtoni*	
	F:AM 27363E	Canidae	Borophaginae	*Aelurodon*	sp.	
	F:AM 50159	Canidae	Borophaginae	*Aelurodon*	sp.	
	F:AM 61725	Canidae	Borophaginae	*Aelurodon*	sp.	
	F:AM 67887	Canidae	Borophaginae	*Aelurodon*	sp.	
	F:AM 67887A	Canidae	Borophaginae	*Aelurodon*	sp.	
	F:AM 67887C	Canidae	Borophaginae	*Aelurodon*	sp.	
	F:AM 67887D	Canidae	Borophaginae	*Aelurodon*	sp.	
	F:AM 67887E	Canidae	Borophaginae	*Aelurodon*	sp.	
	F:AM 67887G	Canidae	Borophaginae	*Aelurodon*	sp.	
	F:AM 67887h	Canidae	Borophaginae	*Aelurodon*	sp.	
	F:AM 67893	Canidae	Borophaginae	*Aelurodon*	sp.	
	F:AM 27364	Canidae	Borophaginae	*Carpocyon*	*webbi*	
	F:AM 27366	Canidae	Borophaginae	*Carpocyon*	*webbi*	

F:AM 27366B	Canidae	Borophaginae	*Carpocyon*	*webbi*
F:AM 27369	Canidae	Borophaginae	*Carpocyon*	*webbi*
F:AM 27370	Canidae	Borophaginae	*Carpocyon*	*webbi*
F:AM 27371	Canidae	Borophaginae	*Carpocyon*	*webbi*
F:AM 27372	Canidae	Borophaginae	*Carpocyon*	*webbi*
F:AM 27475	Canidae	Borophaginae	*Carpocyon*	*webbi*
F:AM 50157	Canidae	Borophaginae	*Carpocyon*	*webbi*
F:AM 61335	Canidae	Borophaginae	*Carpocyon*	*webbi*
F:AM 61336	Canidae	Borophaginae	*Carpocyon*	*webbi*
F:AM 61337	Canidae	Borophaginae	*Carpocyon*	*webbi*
F:AM 61380	Canidae	Borophaginae	*Carpocyon*	*webbi*
F:AM 21110	Canidae	Borophaginae	*Epicyon*	*haydeni*
F:AM 27359A	Canidae	Borophaginae	*Epicyon*	*haydeni*
F:AM 27489	Canidae	Borophaginae	*Epicyon*	*haydeni*
F:AM 61419	Canidae	Borophaginae	*Epicyon*	*haydeni*
F:AM 61555	Canidae	Borophaginae	*Epicyon*	*haydeni*
F:AM 67058	Canidae	Borophaginae	*Epicyon*	*haydeni*
F:AM 67888	Canidae	Borophaginae	*Epicyon*	*haydeni*
F:AM 67888B	Canidae	Borophaginae	*Epicyon*	*haydeni*
F:AM 27362	Canidae	Borophaginae	*Epicyon*	*saevus*
F:AM 61417	Canidae	Borophaginae	*Epicyon*	*saevus*
F:AM 98629	Canidae	Borophaginae	*Epicyon*	*saevus*
F:AM 27376	Canidae	Borophaginae	*Microtomarctus*	*conferta*
F:AM 27377	Canidae	Borophaginae	*Microtomarctus*	*conferta*
F:AM 27378	Canidae	Borophaginae	*Microtomarctus*	*conferta*
F:AM 27392	Canidae	Borophaginae	*Microtomarctus*	*conferta*
F:AM 27393	Canidae	Borophaginae	*Microtomarctus*	*conferta*
F:AM 27398	Canidae	Borophaginae	*Microtomarctus*	*conferta*
F:AM 27398X	Canidae	Borophaginae	*Microtomarctus*	*conferta*
F:AM 27398Y	Canidae	Borophaginae	*Microtomarctus*	*conferta*
F:AM 50172	Canidae	Borophaginae	*Microtomarctus*	*conferta*
F:AM 50184	Canidae	Borophaginae	*Microtomarctus*	*conferta*
F:AM 50185	Canidae	Borophaginae	*Microtomarctus*	*conferta*
F:AM 50186	Canidae	Borophaginae	*Microtomarctus*	*conferta*
F:AM 50203	Canidae	Borophaginae	*Microtomarctus*	*conferta*
F:AM 62770	Canidae	Borophaginae	*Microtomarctus*	*conferta*
F:AM 62772	Canidae	Borophaginae	*Microtomarctus*	*conferta*
F:AM 67339	Canidae	Borophaginae	*Microtomarctus*	*conferta*
F:AM 27380	Canidae	Borophaginae	*Paratomarctus*	*temerarius*
F:AM 27386	Canidae	Borophaginae	*Paratomarctus*	*temerarius*
F:AM 27387	Canidae	Borophaginae	*Paratomarctus*	*temerarius*
F:AM 27389	Canidae	Borophaginae	*Paratomarctus*	*temerarius*
F:AM 27390	Canidae	Borophaginae	*Paratomarctus*	*temerarius*
F:AM 27471	Canidae	Borophaginae	*Paratomarctus*	*temerarius*
F:AM 27472	Canidae	Borophaginae	*Paratomarctus*	*temerarius*
F:AM 27480	Canidae	Borophaginae	*Paratomarctus*	*temerarius*
F:AM 50147	Canidae	Borophaginae	*Paratomarctus*	*temerarius*
F:AM 50148	Canidae	Borophaginae	*Paratomarctus*	*temerarius*
F:AM 50149	Canidae	Borophaginae	*Paratomarctus*	*temerarius*
F:AM 50150	Canidae	Borophaginae	*Paratomarctus*	*temerarius*
F:AM 50151	Canidae	Borophaginae	*Paratomarctus*	*temerarius*
F:AM 50152	Canidae	Borophaginae	*Paratomarctus*	*temerarius*
F:AM 50155	Canidae	Borophaginae	*Paratomarctus*	*temerarius*
F:AM 50158	Canidae	Borophaginae	*Paratomarctus*	*temerarius*
F:AM 67894	Canidae	Borophaginae	*Paratomarctus*	*temerarius*
F:AM 67895	Canidae	Borophaginae	*Paratomarctus*	*temerarius*
F:AM 67901	Canidae	Borophaginae	*Paratomarctus*	*temerarius*
F:AM 67901A	Canidae	Borophaginae	*Paratomarctus*	*temerarius*
F:AM 27476B	Canidae	Borophaginae	*Tomarctus*	sp.
F:AM 67886A	Canidae	Borophaginae	*Tomarctus*	sp.
F:AM 27401	Canidae	Caninae	*Leptocyon*	*vafer*
F:AM 27402A	Canidae	Caninae	*Leptocyon*	*vafer*
F:AM 27402B	Canidae	Caninae	*Leptocyon*	*vafer*
F:AM 27402C	Canidae	Caninae	*Leptocyon*	*vafer*
F:AM 27403	Canidae	Caninae	*Leptocyon*	*vafer*
F:AM 27404	Canidae	Caninae	*Leptocyon*	*vafer*
F:AM 27405	Canidae	Caninae	*Leptocyon*	*vafer*
F:AM 27406	Canidae	Caninae	*Leptocyon*	*vafer*
F:AM 27408	Canidae	Caninae	*Leptocyon*	*vafer*
F:AM 27409	Canidae	Caninae	*Leptocyon*	*vafer*
F:AM 27410	Canidae	Caninae	*Leptocyon*	*vafer*
F:AM 27411	Canidae	Caninae	*Leptocyon*	*vafer*
F:AM 27411A	Canidae	Caninae	*Leptocyon*	*vafer*
F:AM 27411B	Canidae	Caninae	*Leptocyon*	*vafer*
F:AM 27412	Canidae	Caninae	*Leptocyon*	*vafer*
F:AM 27412A	Canidae	Caninae	*Leptocyon*	*vafer*

F:AM 27414	Canidae	Caninae	*Leptocyon*	*vafer*	
F:AM 27414A	Canidae	Caninae	*Leptocyon*	*vafer*	
F:AM 27415	Canidae	Caninae	*Leptocyon*	*vafer*	
F:AM 27416	Canidae	Caninae	*Leptocyon*	*vafer*	
F:AM 27417	Canidae	Caninae	*Leptocyon*	*vafer*	
F:AM 27420	Canidae	Caninae	*Leptocyon*	*vafer*	
F:AM 27421	Canidae	Caninae	*Leptocyon*	*vafer*	
F:AM 27422	Canidae	Caninae	*Leptocyon*	*vafer*	
F:AM 27483	Canidae	Caninae	*Leptocyon*	*vafer*	
F:AM 27486	Canidae	Caninae	*Leptocyon*	*vafer*	
F:AM 30923	Canidae	Caninae	*Leptocyon*	*vafer*	
F:AM 50201	Canidae	Caninae	*Leptocyon*	*vafer*	
F:AM 50202A	Canidae	Caninae	*Leptocyon*	*vafer*	
F:AM 50202B	Canidae	Caninae	*Leptocyon*	*vafer*	
F:AM 62750	Canidae	Caninae	*Leptocyon*	*vafer*	
F:AM 62751	Canidae	Caninae	*Leptocyon*	*vafer*	
F:AM 62752	Canidae	Caninae	*Leptocyon*	*vafer*	
F:AM 62754	Canidae	Caninae	*Leptocyon*	*vafer*	
F:AM 62755	Canidae	Caninae	*Leptocyon*	*vafer*	
F:AM 62756	Canidae	Caninae	*Leptocyon*	*vafer*	
F:AM 62757	Canidae	Caninae	*Leptocyon*	*vafer*	
F:AM 62757A	Canidae	Caninae	*Leptocyon*	*vafer*	
F:AM 62758	Canidae	Caninae	*Leptocyon*	*vafer*	
F:AM 62760	Canidae	Caninae	*Leptocyon*	*vafer*	
F:AM 62761	Canidae	Caninae	*Leptocyon*	*vafer*	
F:AM 62763	Canidae	Caninae	*Leptocyon*	*vafer*	
F:AM 62764	Canidae	Caninae	*Leptocyon*	*vafer*	
F:AM 62765	Canidae	Caninae	*Leptocyon*	*vafer*	
F:AM 62771	Canidae	Caninae	*Leptocyon*	*vafer*	
F:AM 62773	Canidae	Caninae	*Leptocyon*	*vafer*	
F:AM 62774	Canidae	Caninae	*Leptocyon*	*vafer*	
F:AM 62778	Canidae	Caninae	*Leptocyon*	*vafer*	
F:AM 62780	Canidae	Caninae	*Leptocyon*	*vafer*	
F:AM 62790	Canidae	Caninae	*Leptocyon*	*vafer*	
F:AM 62790A	Canidae	Caninae	*Leptocyon*	*vafer*	
F:AM 62791	Canidae	Caninae	*Leptocyon*	*vafer*	
F:AM 62792	Canidae	Caninae	*Leptocyon*	*vafer*	
F:AM 62793	Canidae	Caninae	*Leptocyon*	*vafer*	
F:AM 62824	Canidae	Caninae	*Leptocyon*	*vafer*	
F:AM 62826	Canidae	Caninae	*Leptocyon*	*vafer*	
F:AM 62848	Canidae	Caninae	*Leptocyon*	*vafer*	
F:AM 63136	Canidae	Caninae	*Leptocyon*	*vafer*	
F:AM 67902	Canidae	Caninae	*Leptocyon*	*vafer*	
F:AM 67902A	Canidae	Caninae	*Leptocyon*	*vafer*	
NMMNH P-63414	Canidae	Caninae	*Leptocyon*	*vafer*	
NMMNH P-25405	Canidae	indeterminate	Canidae indet.		
F:AM 27453	Felidae	*incertae sedis*	*Pseudaelurus*	*marshi*	
F:AM 27457	Felidae	*incertae sedis*	*Pseudaelurus*	*marshi*	
F:AM 62135	Felidae	*incertae sedis*	*Pseudaelurus*	*marshi*	
NMMNH P-63413	Felidae	*incertae sedis*	*Pseudaelurus*	*stouti*	
F:AM 27446	Felidae	*incertae sedis*	*Pseudaelurus*	sp.	
F:AM 27451	Felidae	*incertae sedis*	*Pseudaelurus*	sp.	
F:AM 62186	Felidae	*incertae sedis*	*Pseudaelurus*	sp.	
NMMNH P-25182	Felidae	*incertae sedis*	*Pseudaelurus*	sp.	
NMMNH P-63415	Mephitidae	Mephitinae	*Martinogale*	*nambiana*	
USNM 1038	**Mephitidae**	**Mephitinae**	***Martinogale***	***nambiana***	**Holotype**
F:AM 27433	Mephitidae	Mephitinae	*Martinogale*	sp.	
F:AM 27425	Mustelidae	*incertae sedis*	*Brachypsalis*	sp.	
F:AM 27427B	Mustelidae	*incertae sedis*	*Brachypsalis*	sp.	
F:AM 27428	Mustelidae	*incertae sedis*	*Brachypsalis*	sp.	
F:AM 27430	Mustelidae	*incertae sedis*	*Brachypsalis*	sp.	
F:AM 27431	Mustelidae	*incertae sedis*	*Brachypsalis*	sp.	
F:AM 27434	Mustelidae	Mustelinae	*Mustela*	sp.	
F:AM 27443	Mustelidae	Mustelinae	*Mustela*	sp.	
F:AM 27464	Mustelidae	Mustelinae	*Mustela*	sp.	
F:AM 27437	Mustelidae	Mustelinae	*Plionictis*	sp.	
F:AM 27442	Mustelidae	Mustelinae	*Plionictis*	sp.	
F:AM 49215	Mustelidae	Mustelinae	*Plionictis*	sp.	
F:AM 49225	Mustelidae	Mustelinae	*Plionictis*	sp.	
F:AM 62859	Mustelidae	Mustelinae	*Plionictis*	sp.	
F:AM 49223	Mustelidae	Mustelinae	*Sthenictis*	sp.	
NMMNH P-25181	Mustelidae	indeterminate	Mustelidae indet.		
USNM 420649	Mustelidae	indeterminate	Mustelidae indet.		
F:AM 27441	Procyonidae	Procyoninae	*Bassariscus*	sp.	
F:AM 27468	Procyonidae	Procyoninae	*Bassariscus*	sp.	
USNM 167578	Ursidae	Hemicyoninae	*Plithocyon*	*ursinus*	

	USNM 2040	**Ursidae**	**Hemicyoninae**	***Plithocyon***	***ursinus***	**Holotype**
	F:AM 21101	**Ursidae**	**Hemicyoninae**	***Plithocyon***	***ursinus***	**Neotype**
	NMMNH P-25196	indeterminate	indeterminate	Carnivora indet.		
	NMMNH P-25222	indeterminate	indeterminate	Carnivora indet.		
	NMMNH P-25394	indeterminate	indeterminate	Carnivora indet.		
	NMMNH P-25395	indeterminate	indeterminate	Carnivora indet.		
	NMMNH P-25427	indeterminate	indeterminate	Carnivora indet.		
	USNM 420650	indeterminate	indeterminate	Carnivora indet.		
Chama-El Rito						
	F:AM 107736	Canidae	Borophaginae	*Aelurodon*	*ferox*	
	F:AM 61719	Canidae	Borophaginae	*Aelurodon*	*ferox*	
	F:AM 61720	Canidae	Borophaginae	*Aelurodon*	*ferox*	
	F:AM 61731	Canidae	Borophaginae	*Aelurodon*	*ferox*	
	F:AM 61732	Canidae	Borophaginae	*Aelurodon*	*ferox*	
	F:AM 61735	Canidae	Borophaginae	*Aelurodon*	*ferox*	
	F:AM 61737	Canidae	Borophaginae	*Aelurodon*	*ferox*	
	F:AM 67362	Canidae	Borophaginae	*Aelurodon*	*ferox*	
	F:AM 27367	Canidae	Borophaginae	*Aelurodon*	*stirtoni*	
	F:AM 27474	Canidae	Borophaginae	*Aelurodon*	*stirtoni*	
	F:AM 27481	Canidae	Borophaginae	*Aelurodon*	*stirtoni*	
	F:AM 27492	Canidae	Borophaginae	*Aelurodon*	*stirtoni*	
	F:AM 70501	Canidae	Borophaginae	*Aelurodon*	*stirtoni*	
	F:AM 21110	Canidae	Borophaginae	*Epicyon*	*haydeni*	
	F:AM 50181	Canidae	Borophaginae	*Microtomarctus*	*conferta*	
	F:AM 50153	Canidae	Borophaginae	*Paratomarctus*	*temerarius*	
	F:AM 67374	Canidae	Borophaginae	*Paratomarctus*	*temerarius*	
	F:AM 67375	Canidae	Borophaginae	*Paratomarctus*	*temerarius*	
	F:AM 67376	Canidae	Borophaginae	*Paratomarctus*	*temerarius*	
	F:AM 67377	Canidae	Borophaginae	*Paratomarctus*	*temerarius*	
	F:AM 67378	Canidae	Borophaginae	*Paratomarctus*	*temerarius*	
	F:AM 67379	Canidae	Borophaginae	*Paratomarctus*	*temerarius*	
	F:AM 67380	Canidae	Borophaginae	*Paratomarctus*	*temerarius*	
	F:AM 67381	Canidae	Borophaginae	*Paratomarctus*	*temerarius*	
	F:AM 67382	Canidae	Borophaginae	*Paratomarctus*	*temerarius*	
	F:AM 67383	Canidae	Borophaginae	*Paratomarctus*	*temerarius*	
	F:AM 67384	Canidae	Borophaginae	*Paratomarctus*	*temerarius*	
	F:AM 70500	Canidae	Borophaginae	*Paratomarctus*	*temerarius*	
	F:AM 104813	Canidae	Borophaginae	*Tomarctus*	sp.	
	F:AM 49246	Mustelidae	Mustelinae	*Sthenictis*	sp.	
Ojo Caliente						
	F:AM 67370	Canidae	Borophaginae	*Aelurodon*	*ferox*	
	F:AM 67371	Canidae	Borophaginae	*Aelurodon*	*ferox*	
	F:AM 67372	Canidae	Borophaginae	*Aelurodon*	*ferox*	
	F:AM 67887F	Canidae	Borophaginae	*Aelurodon*	sp.	
	F:AM 67888A	Canidae	Borophaginae	*Aelurodon*	sp.	
	F:AM 70502	Canidae	Borophaginae	*Carpocyon*	*webbi*	
	F:AM 104813	Canidae	Borophaginae	*Paratomarctus*	*temerarius*	
	F:AM 67369	Canidae	Borophaginae	*Paratomarctus*	*temerarius*	
	F:AM 62766	Canidae	Caninae	*Leptocyon*	*vafer*	
	F:AM 62767	Canidae	Caninae	*Leptocyon*	*vafer*	
	F:AM 62768	Canidae	Caninae	*Leptocyon*	*vafer*	
	F:AM 62769	Canidae	Caninae	*Leptocyon*	*vafer*	
Dixon						
	F:AM 67047	Canidae	Borophaginae	*Aelurodon*	*taxoides*