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ARTICLE

ANATOMY OF THE POSTCRANIAL SKELETON OF “*MIACIS*” *UINTENSIS* (MAMMALIA: CARNIVORAMORPHA)

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ABSTRACT—This paper provides the first detailed description of the only known postcranial skeletal elements of “*Miacis*” *uintensis*. The morphology of the skeleton differs markedly from previously described “miacids” (a paraphyletic assemblage of early fossil carnivoramorphans), invalidating the notion that all “miacids” were very similar in their postcranial morphology and locomotor styles. The majority of the differences indicate an animal less well adapted to an arboreal lifestyle than has been inferred for other early “miacid” carnivoramorphans. A phylogenetic analysis clearly nests “*Miacis*” *uintensis* within the paraphyletic array of taxa previously referred to as the “Miacidae,” in a position closer to the crown clade Carnivora than is *Vulpavus*, a “miacid” whose postcranium has been previously described. When compared with the early canid *Hesperocyon*, this specimen shares many features thought to relate to the acquisition of a more terrestrial mode of life. This result indicates that, in contrast to prior models suggesting arboreality for all “miacids,” at least one independent ‘descent from the trees’ occurred much earlier within the array of stem carnivoramorphan taxa.

INTRODUCTION

Historically, all fossil Carnivora relatives from the Paleocene and Eocene that possessed upper and lower third molars were united in the family Miacidae. Recent phylogenetic analyses have recognized the “Miacidae” as a paraphyletic assemblage of carnivoramorphan stem taxa on the branch leading to crown clade Carnivora, following the divergence of the Viverravidae, the other group of early Cenozoic carnivoramorphans (Wesley–Hunt and Flynn, 2005; Wesley–Hunt and Werdelin, 2005). Since the pioneering phylogenetic work of Matthew (1909), the position of both groups has been uncertain (see more detailed discussions in Flynn and Galiano, 1982; Flynn et al., 1988; Wyss and Flynn, 1993; Flynn and Wesley–Hunt 2005). Most previous studies placed the “Miacidae” in one of several alternative positions: basal within Caniformia (Flynn and Galiano, 1982) or as stem taxa to the living Carnivora, either outside a Viverravidae+ Carnivora clade (Wyss and Flynn, 1993) or closer to Carnivora than to Viverravidae (Bryant, 1991). None of these studies explicitly tested the assumption of monophyly of either the “Miacidae” or Viverravidae. The recent cladistic analysis of Wesley–Hunt and Flynn (2005) surpassed previous studies in terms of breadth of taxon sampling and number of characters. Perhaps most importantly, instead of the composite (or presumed monophyletic) “Miacidae” terminal OTU used in prior studies, individual members of this group were included as species–level terminal taxa. A topology in which “Miacidae” is monophyletic requires two additional steps using that matrix (Wesley–Hunt and Flynn, 2005), providing modest support for the most parsimonious hypothesis of relationships generated, in which a monophyletic Viverravidae was the outgroup to all remaining Carnivoramorpha (and a paraphyletic series of “miacid” taxa were sequentially nearer outgroups to crown clade Carnivora). These tests have also shown us that even the genus “*Miacis*” is not monophyletic.

Consequently, understanding the morphology and phylogenetic relationships of various taxa traditionally included within the “Miacidae” is essential for a firm grasp of the ancestral anatomical conditions of the Carnivora. As more time is devoted to their study and more new taxa are discovered, it is likely that many features now thought to be novel in basal members of crown clade Carnivora will be found to be synapomorphies arising deeper within the phylogeny or to occur earlier and independently within various taxa previously assigned to the paraphyletic “Miacidae.” In this paper we use “Miacidae” or “miacids” in quotation marks to reflect paraphyly of these previously proposed groups, and the terms Carnivora to refer solely to the crown clade and Carnivoramorpha to the crown clade plus the early stem taxa that are more closely related to Carnivora than to any other living mammals or to the extinct creodonts (following Wyss and Flynn, 1993 and Flynn and Wesley–Hunt, 2005).

“Miacids” are represented by a modest number of postcranial skeletons in collections. Unfortunately, many of these specimens are only partly described (e.g., Gingerich, 1983; Wesley and Flynn, 2003) or entirely undescribed, with only two recent detailed studies of the postcranial skeleton of “miacids” (Heinrich and Rose, 1995, 1997) and two others for Viverravidae (Heinrich and Rose, 1997; Heinrich and Houde, 2006). These rare in–depth studies have resulted in the assumption of a generalized postcranial morphology and arboreal locomotor mode for the “Miacidae,” probably due to the then–dominant notion that it was a monophyletic clade, and possibly basal to Carnivora. Now that the paraphyletic nature of the group has been recognized, it is prudent to re–examine the postcranial morphology of various stem carnivoramorphans in detail, as has recently been done for the craniodental morphology of many of these taxa (e.g., Wesley and Flynn, 2003; Wesley–Hunt and Flynn, 2005; Wesley–Hunt and Werdelin, 2005; Polly et al., 2006). Of particular interest is the genus “*Miacis*,” which itself is likely to be non–monophyletic, as it appears to be a “wastebasket” assemblage of varied taxa often thought to possess relatively primitive features for the Carnivoramorpha. In recent studies, members of “*Miacis*” have been found to lie in various places near the base of the Carnivor-

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amorpha radiation, with one species (“*M.*” *cognitus*) even falling within the Carnivora as an early member of the Caniformia (Wesley–Hunt and Flynn, 2005).

Generalizations of postcranial morphology based on few taxa or without incorporation of a phylogenetic framework may discard information on stem carnivoramorphan evolution. This study addresses that possibility by describing the skeletal anatomy of an undescribed, relatively complete taxon typically considered to be a “miacid”: AMNH 1964, incorporating it into a broader phylogenetic analysis, examining the functional implications of various individual postcranial features, and making inferences about the possible locomotor mode of this taxon. This specimen was collected in 1895 from the White River locality, “Upper Uinta” (Matthew, 1909), in Utah, roughly 39–42 million years in age (Janis et al, 1998). It was referred to *Miacis uintensis* by Matthew (1909) and the specimen agrees closely with Osborn’s (1895) original description of the species: its p4 lacks a complete cingulum, m1 has a broad talonid which is elevated on the buccal edge, m2 is reduced but still possesses a complete talonid, and m3 is highly reduced. AMNH 1964 also agrees in size with the type specimen of “*Miacis*” *uintensis*, and it is distinctively larger than most other “miacids.”

The taxonomic history of this species is complicated. It was originally named as *Miacis uintensis* by Osborn (1895). Matthew (1899) subsequently formed the genus *Prodaphaenus* by amalgamation of some previously named species, including *P. scotti* and this species (as *P. uintensis*). Later Matthew (1909) considered *P. scotti* and *P. uintensis* to be only distantly related to one another and moved *P. uintensis* back to “*Miacis*.” Current confusion resides, in part, in the state of taxonomy for *Prodaphaenus*. For decades the type species was considered to be *Prodaphaenus scotti*, but Bryant (1992) pointed out that this was incorrect. When *Prodaphaenus* was first designated (Matthew, 1899), *P. scotti* had not even been formally described, as a valid description was only offered later that year (Wortman and Matthew, 1899). Thus at the time *Prodaphaenus* was named,”*Miacis*” *uintensis* was the only “originally included nominal species” (Bryant, 1992). Bryant (1992) applied the prior subgeneric name *Miocyon* for “*P.*” *scotti (Miocyon scotti)*. Therefore, the name *Prodaphaenus*, if considered to be a valid taxon, would have “*Miacis*” *uintensis* as the type species of the genus. Herein, this taxon is conservatively referred to as “*Miacis*” *uintensis*, as more detailed systematic work is necessary to ascertain the validity of removal of this species to a taxon separate from a clade containing the type species of *Miacis* and possibly other species. While this species, represented by AMNH 1964, was incorporated into the matrix of Wesley–Hunt and Flynn (2005), many other early Cenozoic “miacoid” taxa have not yet been included in a comprehensive analysis of the phylogeny of basal carnivoramorphan species, precluding a reliable assessment of the relative interrelationships of the various basal carnivoramorphan taxa.

Since the discovery and collection of AMNH 1964, its only mention in the literature was two paragraphs in Matthew’s (1909) Bridger Basin monograph, where he mentioned the rather “aberrant form” of this specimen. Herein the postcranial morphology is described for the first time. The dentition is also described in detail, and the specimen is coded for preliminary phylogenetic analyses (based on cranio–dental characters) from the partially prepared skull.

Materials and Methods

Descriptions of AMNH 1964 are based on direct examination of the specimen, housed in the fossil mammal (FM) collections of the American Museum of Natural History, where it was originally part of the Cope collection. Comparisons to other “miacids” were conducted using published descriptions of *Miacis petilus* (Heinrich and Rose, 1995) and *Vulpavus* (Heinrich and Rose, 1997). The specimens of *Vulpavus* were not identified to species level by Heinrich and Rose (1997), but each was tentatively identified as either *V. canavus* or *V. australis* based upon stratigraphic location. Comparisons were facilitated by direct examination of specimens of *Vulpavus profectus* (AMNH 12626) and *Vulpavus palustris* (AMNH 11498). Institution abbreviations used are:AMNH – American Museum of Natural History, New York, NY, and USGS – US Geological Survey, Denver, now housed at the Dept. of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

The phylogenetic position of the taxon represented by AMNH 1964 was determined by coding it for the characters and including the taxa in the matrix of Wesley–Hunt and Flynn (2005). Other basal carnivoramorphans, *Quercygale* and *Viverravus acutus*, were incorporated based upon the coding provided by Wesley–Hunt and Werdelin (2005) and Polly et al. (2006), respectively. This is the first time that “*M.*” *uintensis* has been included in a broader phylogenetic analysis of Carnivoramorpha. The final matrix included 43 taxa coded for 99 characters. Due to possible non–independence of characters 43 and 44 (concerning the relationships of the metastyle and parastyle of M1) of Wesley–Hunt and Flynn (2005), Wesley–Hunt and Werdelin (2005) combined those characters to make a single unordered three state character. The analysis conducted here dealt differently with this. As character 43 (metastyle length) did not vary among included carnivoramorphans while character 44 (parastyle length) did, character 43 was eliminated from the analysis. This elimination had no effect on the resulting topology. Numbering of characters was kept the same as in Wesley–Hunt and Flynn (2005) to reduce possible confusion. Character 40 was the only multistate character that was ordered, based on the conditions specified in the original study. The scoring used for AMNH 1964 is given in Table 1.

TABLE 1. Coding of AMNH 1964 for matrix of Wesley-Hunt and Flynn (2005)

1??0???000 0011?11112 1?11000101 0001000?11 ?01100?1?? ?0?1011?1? ???0?00?0? ?0???????? 010?01?0?? 0??0?????

The analysis was conducted in PAUP* version 4.0b (Swofford, 2000). The heuristic search option was used with TBR branch swapping. 1000 replicates were run to maximize the probably that the most parsimonious tree was recovered. Bootstrap values were generated with the same program, via 1000 bootstrap replicates with 10 internal trials each. Decay index values were generated using TreeRot (Sorenson, 1999).

Reconstructions of ancestral locomotor conditions were generated using Mesquite v2.01 (Maddison and Maddison, 2007). This was accomplished by creating a small matrix in Mesquite, using the OTUs seen in Figure 3 and a single multistate character of locomotor styles, information for locomotor habits of the included creodont taxa come from Polly (1996) and Gebo and Rose (1993). The tree used comes from a pruned version of the strict consensus tree generated by this analysis, combined with the outgroup creodonts. Carnivoramorpha and the two subclades of Creodonta are left in a polytomy, following the method of Flynn and Wesley–Hunt (2005). The locomotion character was then mapped upon the tree, and using the parsimony character mapping functionality of Mesquite, states of the internal nodes were reconstructed. To test the robustness of this method two versions of the character were used, one in which scansoriality was its own separate unique state, and the other in which scansority was represented by a polymorphic state assignment of ‘01.’

DESCRIPTION

AMNH 1964 is the only known postcranial skeleton of “*Miacis*” *uintensis*. It preserves several cervical and caudal vertebrae,

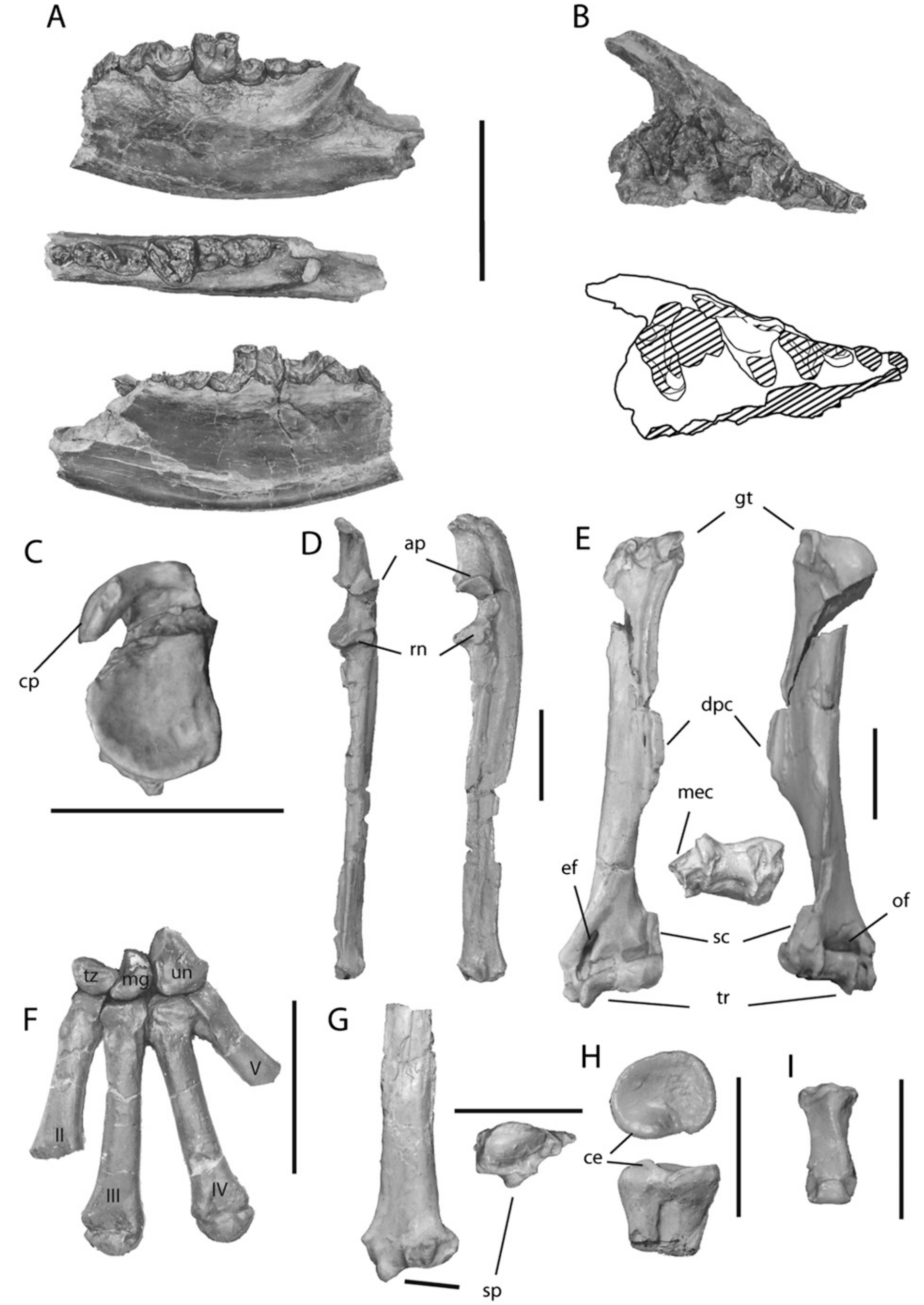

FIGURE 1. AMNH 1964, "*Miacis" uintensis*, dentition and forelimb elements. **A**, fragment of p3-m3 of left lower jaw of AMNH 1964 in buccal, occlusal, and lingual view; **B**, occlusal view of right maxilla containing P3-M1 with fragment of m1 between P4 and M1 in photograph and line drawing; **C**, glenoid of left scapula; **D**, left ulna in anterior and lateral view; **E**, left humerus in anterior, distal, and posterior-lateral view; **F**, left manus in dorsal view; **G**, distal left radius in anterior and distal view; **H**, proximal left radius in proximal and anterior view; **I**, middle phalanx in dorsal view, uncertain attribution to manus or pes. **Abbreviations: II-V**, metacarpals; **ap**, anconeal process; **ce**, capitular eminence, **cp**, coracoid process; **dpc**, delto-pectoral crest; **ef**, entepicondylar foramen; **gt**, greater tubercle; **mec.** medial epicondyle; **mg**, magnum; **of**, olecronon fossa; **rn**, radial notch;, **sc**, supinator crest; **sp**, styloid process; **tr**, trochlea for ulna articulation; **tz**, trapezoid; **un**, unciform. Scale bars equal 2 cm.

scapula fragments, left humerus, left ulna, left radius fragments, elements of the left manus, fragments of the left pelvis, an almost complete right femur, distal left femur, left tibia and fibula, left calcaneus, right and left astragalus, and right navicular, cuboid, and ectocuneiform. Figures 1 and 2 show many of the skeletal elements in the following description and Tables 2 and 3 gives standard measurements of long bones and the two major ankle bones.

Scapula—A fragment of the left scapula remains embedded in matrix (Fig. 1C). A large acromion process is present, extending just over the edge of the glenoid fossa. It is possible that this process extended further, but its full extent cannot be ascertained due to breakage. Although a clavicle was not recovered as part of this specimen, the length of the acromion process implies the presence of a clavicle (Wang, 1993). This bone is reduced in most crown clade Carnivora, but is of uncertain

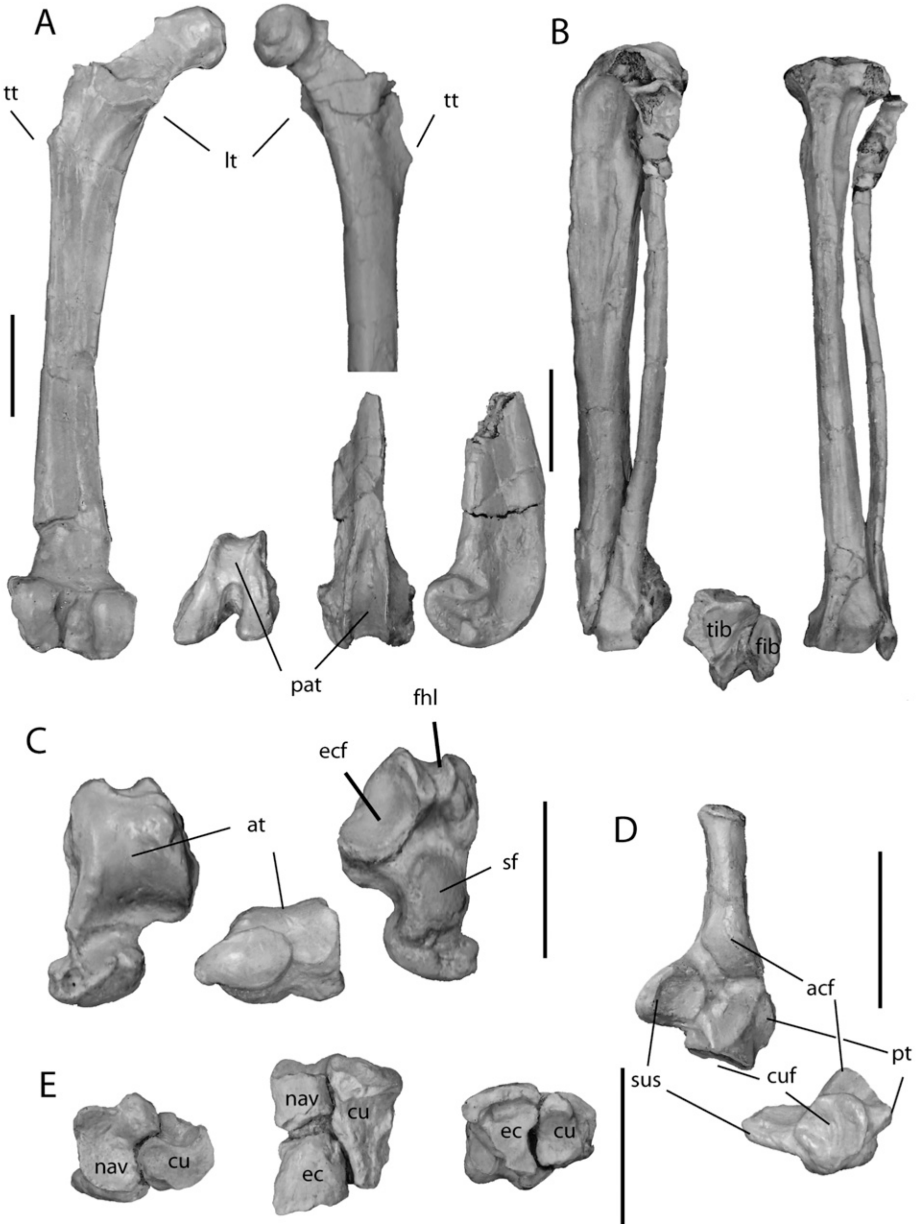

FIGURE 2. AMNH 1964, *"Miacis" uintensis*, hindlimb elements. **A**, left femur in posterior and anterior view and distal right femur in distal, anterior, and lateral view; **B**, left tibia and fibula in lateral, distal, and anterior views; **C**, left astragalus in dorsal, anterior, and ventral view; **D**, left calcaneus in dorsal and anterior view; **E**, left navicular, cuboid, and ectocuneiform in dorsal, anterior, and ventral view. **Abbreviations: at**, astragalar trochlea; **acf**, astragalocalcaneal facet; **cu**, cuboid; **cuf**, cuboid facet; **ec**, ectocuneiform; **ecf**, ectal facet; **fib**, fibula; **fhl**, groove for tendon; **lt**, lesser trochanter; **nav**, navicular; **pat**, patellar trochlea; **pt**, peroneal tubercle; **sf**, susentacular facet; **sus**, susentaculum; **tib**, tibia; **tt**, third trochanter. Scale bars equal 2 cm.

development in basal carnivoramorphans. The glenoid fossa is round and shallow; the supraglenoid tubercle is not expanded outwards to create a deepening effect. A well–developed coracoid process is present. The scapula is heavily damaged posterior to the glenoid fossa, but it appears that there was not a well–developed scapular notch.

Humerus—The left humerus is broken (Fig. 1E). The proximal portion of this bone reveals the start of a high deltopectoral crest, a moderately developed lesser tubercle, and a greater tubercle that fails to rise above the level of the humeral head. The exact angle between the greater and lesser tubercles cannot be estimated, due to an uncertain amount of post–mortem deformation of the bone.

The distal portion of the left humerus has undergone some minor plastic deformation. The deltopectoral crest is very well developed, and at its apex it was high enough to roughly double the anterior–posterior depth of the bone. This crest reaches its apex immediately distal to the broken contact with the proximal portion, near the midshaft, and maintains an even height for about 1.25 cm after which its height rapidly declines. The apex of the deltopectoral crest is roughly at the midpoint of the shaft and it decreases in size shortly before reaching the lower third of the bone. A well-developed supracondylar ridge is present. Despite damage to this feature, the pattern of breakage suggests that it extended along the shaft proximal to the level at which the deltopectoral crest ends distally. The base of the ridge follows

TABLE 2. Measurements of postcranial elements of AMNH 1964. All measurements are in centimeters.

	Humerus	Ulna	Femur	Tibia	Fibula	Calcaneus	Astragalus
Greatest length	9.87	10.2	12.9	11.68	11.01	3.24	2.22
Greatest width	x	x	x	x	x	1.88	1.66

the lateral edge of the shaft and shows no signs of curving completely around to the posterior surface of the humerus; the crest clearly ends on the lateral side of the shaft. Distally, the supracondylar ridge feature appears to have been distorted post-mortem, such that it curves sharply anteriorly, but it is reasonable to assume that it originally lay in the same plane as the trochlea and capitulum, due to the presence of fractures in the surface of the bone indicating folding and the unnatural 90 degree angle of the structure. A shallow, ovoid radial fossa is present and separated from an equally shallow coronoid fossa by a gently sloping ridge of bone. There is a large entepicondylar foramen, the medial border of which runs at roughly a 45° angle relative to the main shaft. The medial epicondyle has been broken off where the medial border of the entepicondylar foramen would join it, so its morphology is unknown. The preserved part of the neck indicates that the medial epicondyle was not in line with the articulation for the radius and ulna, but rather was angled posteriorly.

The capitulum and trochlea are continuous, not separated by a small ridge of bone as in some other early carnivoramorphan taxa. The distal end of the bone has been slightly distorted, with the condyles pushed upon the anterior surface of the bone; the pre–distortion condition likely would have shown the articular surfaces to be in the same anterior–posterior plane as the shaft, as the trochlea is mostly in line with the shaft, and both epicondyles are in line with the shaft, which is the typical condition seen in other “miacids.” The trochlea extends more distally than the capitulum, with A sharp projection on its medial boundary. A clear ‘L’–shaped ridge can be seen on the distal end of the capitulum, and a slight depression occurs on its roughly cylindrical, but slightly swollen proximal surface, in the same mediolateral plane as this ridge. The posterior ulnar articulation surface is clearly bordered by ridges of bone on both edges. A small pit for the ulnar collateral ligament lies medially to the medial ridge. The olecranon fossa is deep and slot–like, with no traces of a supratrochlear foramen, although this region is somewhat plastically distorted.

Ulna—The left ulna is complete, with only minor breakage of its distal end (Fig. 1D). The most notable post–mortem deformation is a moderate mediolateral compression of the olecranon process. A groove for the *m. triceps brachii* tendon is present on the proximal end. There is very little anterior curvature of the olecranon process. The semilunar notch is 0.57 cm deep and a strong, shelf–like anconeal process forms the proximal border. The radial notch is almost totally flat, long, narrow, and oriented anterolaterally. The *m. brachialis* insertion site is readily visible on the anterior edge of the shaft, situated medially and distally to the coronoid process. The shaft is straight, and near its distal end its cross–sectional shape shifts from relatively round to triangular, due to the presence of medial and lateral flanges (the medial is more strongly developed). The posterior surface of the bone is broad and relatively uniform in width. While badly damaged otherwise, the distal end does preserve a spur of bone on its lateral edge.

Radius—The proximal end and the distal half of the left radius are present in AMNH 1964 (Fig. 1G, H). The surface of the head is slightly ovoid (0.88 cm anteroposteriorly x 1.08 cm mediolaterally), with a notable capitular eminence adjacent to an indentation in the rim. Nothing can be said about the orientation of the proximal surface compared to the shaft, due to missing parts of the shaft. The distal radius is somewhat compressed anteroposteriorly, and has a robust, clearly defined styloid process. The distal ulnar facet is highly concave, and the extensor tubercle of the radius is angled slightly anteriorly.

Manus—The right manus is partially preserved (Fig. 1F). The unciform is triangular. The magnum and trapezoid are similar in size and shape, both being flattened ovals. There is no scaphoid or lunar (nor a fused scapholunar). Also recovered were the metacarpals of digits II–V. Metacarpals III–IV are complete, with a length/width radio of 7.0 for digit III (measuring width at the midpoint of the shaft). The metacarpals are somewhat compressed dorsoventrally and they have fairly spherical distal ends.

Phalanx—One right middle phalanx is preserved (Fig. 1I). It is unknown if this phalanx belongs to the manus or pes, but as all other distal autopodial elements preserved are from the forelimb, the preserved phalanx is most likely from the manus. Even though it is but an isolated middle phalanx, it is noteworthy in that it possesses a non-symmetrical dorsal surface. A ridge runs along the dorsal surface towards what appears to be the medial margin, creating a large depression on the external side. This feature has been correlated with the presence of retractable claws in other carnivoramorphans (e.g., Wesley and Flynn, 2003).

Pelvic Girdle—Only a small part of the pelvis is present (a piece of the right acetabulum and part of the right ilium), and it is very poorly preserved. The only salient details that can be observed are the presence of a robust anterior inferior iliac tubercle and that the dorsal margin of the acetabulum is roughly even with the dorsal surface of the pelvis.

Femur—The left femur is complete, except for missing the lateral margin of the proximal end and slight damage to the patellar trochlea; this region is preserved in the fragment of the right femur, however (Fig. 2A). There is a broad articular surface on the femoral head, extending almost to the base of the neck. The fovea capitis is located roughly in the middle of the head, directed more medially than proximally. The greater trochanter is not preserved. The lesser trochanter projects posteromedially, and although it is damaged there is clear evidence of the presence of a third trochanter, positioned slightly distally when compared to the lesser trochanter. The curvature of the shaft is hard to determine, as the bone is somewhat deformed, but it appears to have been relatively straight. The patellar groove is narrow and bound on both sides by high ridges. There is a distinct fossa on the medial epicondyle; above this lies a second, less well–defined indentation. The posterior surfaces of the condyles are flush with the main body of the shaft.

Tibia—The left tibia is complete except for slight damage to its distal end (Fig. 2B). A fragment of the proximal end of the right tibia is also present, but it is severely distorted. The medial condyle is concave and is positioned slightly lower than the convex lateral condyle. Neither condyle’s inner border projects

TABLE 3. Measurements of metacarpal III of AMNH 1964. All measurements are in centimeters.

	Length	Width of proximal end	Height of proximal end	Midshaft width	Midshaft height	Width of distal end
Metacarpal III	2.85	.46	.66	.39	.34	.66

far proximally, and there is a distinct valley separating the pair. On the posterior surface there is a deep groove on the lateral side of the shaft, possibly for the origin of the *m. tibialis posterior* (Heinrich and Rose, 1997). The cnemial crest is prominent (although this may be slightly exaggerated due to the moderate lateral compression of the bone) but is absent below the upper third of the shaft. The shaft has a circular cross section after the crest diminishes, and a raised tubercle is present on its medial side, near the proximal end. The distal end of the bone has few distinct features, save for a prominent interosseous tubercle, and a posterior projection. The tibia–astragalus articular surface is smooth, measuring 0.71 cm (mediolateral) by 1.14 cm (anteroposterior).

Fibula—The left fibula is present, still bound to the tibia by matrix (Fig. 2B). This bone is rather featureless, with a slender, straight shaft. Details of its proximal and distal ends are not observable because of distortion and matrix attaching it to the tibia.

Pes—The left astragalus and calcaneus are both excellently preserved (Fig. 2C–E). Additional less well–preserved foot elements include the right astragalus, and left cuboid, navicular, and ectocuneiform.

The astragalus has a broad, generally flat dorsal surface for articulation with the distal tibia, with only a shallow trochlear groove present along its midline. In contrast, its posterior surface is deeply grooved, presumably for passage of the *flexor fibularis* tendon. This groove is roughly in line with the groove on the dorsal surface. A dorsally oriented astragalar foramen lies just anterior to this deep groove. The medial surface displays a well-defined malleolar sulcus. The lateral surface, for articulation with the fibula, is dorsoventrally deep, more so anteriorly than posteriorly. On the ventral surface, the sustentacular facet is well defined, convex, and separated from the deeply concave ectal facet. The astragalar head is well defined anterior to a narrow neck. The astragalar head has a somewhat rounded shape in dorsal view, with a very slightly convex surface for articulation with the navicular, and is tear–drop shaped in distal view.

A long, mediolaterally compressed tuber calcanei forms more than half the length of the calcaneus. The posterior calcaneal facet of the calcaneus articulates with the ectal facet. The facet for articulation with the sustentacular facet of the astragalus is large and slightly concave. The peroneal tubercle is small, forming only a slight bump on the distal lateral margin of the bone. The facet for the cuboid lies very close to these two processes, is slightly concave, and faces medially relative to the long axis.

The left cuboid, navicular, and ectocuneiform still are held together by matrix, offering information about their positions relative to one another, but obscuring many morphological details. The navicular is roughly circular in proximal view, with a large posterior tubercle, and joined with the ectocuneiform along most of its distal surface, leaving only a small region medially for articulation with the mesocuneiform and entocuneiform. The navicular articulates with the cuboid on its external margin. The cuboid connects to both the navicular, via a short process, and to the ectocuneiform. It is longer than it is wide, wider proximally than distally, and with a smooth distal surface for articulation with metatarsal IV and a smaller, more laterally orientated surface for articulation with metatarsal V. The ectocuneiform has a square dorsal face, with a 'lip' that overhangs its main body. Medially it has a slightly concave articulation surface for the mesocuneiform, and distally it has a characteristic 'T'–shaped surface for articulation with metatarsal III.

Vertebrae—Several cervical and caudal vertebrae are present. A fragment of the atlas provides little useful morphological information, and it is only definitively identifiable as an atlas due to its articulation with the occipital condyle. The axis is severely compressed dorso–ventrally, thus preserving few distinct features other than its characteristic dens process. The rest of the cervical vertebrae remain articulated within matrix. Their ventral surfaces are exposed, showing small ridges along the midlines. Transverse foramina are present in the bases of the short transverse processes. The caudal vertebrae are much longer than wide, and all structures on the vertebral body are extremely reduced or absent, suggesting a long tail.

Comparison to Other Early Cenozoic Basal Carnivoramorphans

Among early Cenozoic basal carnivoramorphans, postcrania have been analyzed in detail for only four taxa; two viverravids and two members of the paraphyletic stem lineage previously grouped as "miacids." As noted above, AMNH 1964 has dental features indicating that it is assignable to "*Miacis*" *uintensis*, as recognized by Matthew (1909) when he first mentioned the craniodental material pertaining to this specimen and assigned them to this species. Herein we refer either directly to the specimen number or to the taxon name ("*M.*" *uintensis*) interchangeably, as this is the only known postcranium for this species.

"*Miacis*" *uintensis* is much larger than the previously described *M. petilus* (Heinrich and Rose, 1995) and *Vulpavus* (Heinrich and Rose, 1997). Body mass was reconstructed using regressions of m1 area (Legendre and Roth, 1988). We estimate the body mass of "*M.*" *uintensis* was 5.15 kg. Previously published weight estimates of *M. petilus* and *Vulpavus* were not based upon dental measurements, but rather on limb bone dimensions. Weight estimates using the limb bones were not appropriate to apply to AMNH 1964 due to the post–mortem distortion of these elements. To assure comparable estimates of body mass, weights were generated for previously described specimens based solely on m1 area. The m1 area of *M. petilus* was generated by measuring USGS 7161, providing a body mass estimate of 0.94 kg. A mean body mass estimate of 1.47 kg for both *V. australis* and *V. canavus* was generated by averaging the estimates for several of the specimens figured and discussed in Heinrich and Rose (1997), as these specimens were not specifically allocated to either species, only attributed as belonging to one of these two species. The regression equation used was from Legendre and Roth (1988) and is as follows: $\ln \text{mass} = 1.653 (\text{area of m1 in mm}^2) + 1.897$. We note that the body mass estimates based upon the dentition are higher than those based on cross sectional area of limb bones; roughly double for "*M.*" *petilus* and over three times greater for *Vulpavus*.

The two viverravids previously examined in detail were *Didymictis protenus* (Heinrich and Rose, 1997) and *Viverravus acutus* (Heinrich and Houde, 2006). These papers revealed that the postcranial morphology is not uniform among the SE taxa studied within the monophyletic Viverravidae. General comparisons between the "miacids" examined in this paper and published descriptions and illustrations of the two species of Viverravidae reveal that *V. acutus* is more similar to the "miacids" than is *D. protenus*. Within the Viverravidae, hindlimb morphology in these two species is more similar than that of their forelimbs. The ancestral conditions of the postcranial skeleton of the Viverravidae cannot be reconstructed at present, due to their great anatomical distinction and this sparse sample of previously studied taxa. Accordingly, detailed comparisons to these two morphologically disparate taxa would not refine reconstructions for ancestral conditions for the clade of the remaining basal carnivoramorphan species ("Miacidae") plus crown clade Carnivora. A more informative and useful comparative analysis will be conducted after future work has incorporated more taxa and better constrained the primitive conditions for both the Viverravidae and the other basal carnivoramorphans. It can be stated, however, that overall "*Miacis*" *uintensis* resembles the studied Viverravidae in regards to hindlimb, most notably the femur, more than it does the "miacids" with which we shall now compare it.

Forelimb—The fragments of the scapula agree with the generalized anatomy previously attributed to "miacids," with a long acromion process overhanging the glenoid fossa. The humerus also is similar to that reported for *Vulpavus* and *Miacis petilus* in the high laterally leaning deltopectoral crest, low greater tubercle, presence of the entepicondylar foramen, no clear ridge of bone separating the trochlea from the capitulum, and small ulnar collateral ligament 'pit.' AMNH 1964 differs from *Vulpavus*, and agrees with *M. petilus*, in having the medial trochlea rim extending markedly beyond the capitulum distally. AMNH 1964 differs from *M. petilus*, however, in that the supracondylar ridge does not curve around to the ventral surface of the shaft (the state of this feature has not been reported previously for *Vulpavus*). "*M.*" *uintensis* (AMNH 1964) differs from both other taxa in its very slight development of the coronoid and radial fossae, and its very deep and slot–like olecranon fossa.

The ulna agrees with both *Vulpavus* and *Miacis petilus* in the flattened antero-laterally directed radial notch, the *m. brachialis* insertion scar, and the paired flanges on the distal region. AMNH 1964 differs from both *Vulpavu*s and *M. petilus* in the lack of curvature of the anterior margin of the olecranon and the much greater development of the anconeal process. The radius can only be compared with that of *Vulpavus*, as that element in *M. petilus* has not been described. The bones in "*M.*" *uintensis* and *Vulpavus* are congruent in the circular shape of the radial head (although this feature is slightly more ovoid in "*M.*" *uintensis*) the morphology of the distal shaft, size of the ulnar facet, and angle and size of the extensor tubercle. "*M.*" *uintensis* differs in having a larger capitular eminence and a more concave ulnar facet. There are no published descriptions for other early carnivoramorphans of the carpal bones that are present in AMNH 1964, nor any manus for *M. petilus*, precluding comparisons among these taxa. The metacarpals agree in appearance with those of *Vulpavus*, with perhaps less dorsoventral flattening of these bones in *Vulpavus*.

Hindlimb—The small preserved portion of the innominate is consistent with that observed in *Vulpavus* and *Miacis petilus*. The femur is similar to both of those previously described "miacids" in possessing a third trochanter, having a straight femoral shaft, and similar condylar morphology. The femur of AMNH 1964 differs from that in both *Vulpavus* and *M. petilus* by having a more centered fovea capitis, more posteriorly angled lesser trochanter, more elongated femoral neck, and narrower patellar trochlea with higher bounding ridges. The tibia morphology is consistent with both of the other "miacid" taxa in having a posterior depression, tubercle on the medial surface, interosseous tubercle, and smooth undivided distal articular surface for the astragalus. The fibula does not differ in any notable way.

The astragalus has been described for *Vulpavus* (Heinrich and Rose, 1997), *Miacis exiguus* (Gingerich, 1983) and *Uintacyon rudis* (Gingerich, 1983). The astragalus of AMNH 1964 is congruent with those taxa in all noted morphological features, except for the depth of the groove for the flexor hallucis longus tendon, which is much deeper in "*M.*" *uintensis* than in previously described taxa. Additionally the broad surface for articulation with the fibula resembles that of *U. rudis* and *Vulpavus*, whereas *M. exiguus* has a much less dorsoventrally deep surface. The calcaneus has been described previously only for *Vulpavus*. AMNH 1964 is generally similar in form, other than that the sustentaculum is slightly curved dorsally, the posterior calcaneal facet faces more dorsally, and the distal peroneal tubercle is less well developed in AMNH 1964. The cuboid agrees with the description of that in *Vulpavus*, as it is also wider at its proximal surface than at its distal surface, and has a much smaller and laterally facing articulation surface for metatarsal V relative to that of metatarsal IV. Additional comparisons of the morphology of the medial edge cannot be made yet, as the cuboid is still joined to the navicular and ectocuneiform. The remaining tarsal bones preserved in AMNH 1964 cannot be compared to the other taxa, as there are no previous descriptions of these elements in other "miacids."

Phalanx—Previously published descriptions of the middle phalanx of *Vulpavus* (Heinrich and Rose, 1997) and *Tapocyon* (Wesley and Flynn, 2005) are available for comparisons. The asymmetrical nature of the phalanx in AMNH 1964 is entirely absent from *Vulpavus*, while *Tapocyon*'s shaft is more similar to AMNH 1964 but has a more elaborately developed asymmetry of the distal articulation surface.

Vertebrae—The only descriptions available for comparison are those of caudal vertebra of *M. petilus* (Heinrich and Rose, 1995). Those vertebrae agree closely with those in AMNH 1964.

Functional Morphology and Locomotor Inferences

The forelimb of AMNH 1964 offers several clues as to the locomotor habits of "*Miacis*" *uintensis*. The large acromion process of the scapula is thought to indicate a strong acromiodeltoid muscle for abduction, as seen in many viverrids that spend substantial time in the trees (Taylor, 1974), and a well-developed clavicle (Wang, 1993). A functional clavicle, in turn, implies increased lateral mobility of the forelimb (Jenkins, 1974). The high and long deltopectoral crest in "*M.*" *uintensis*, reminiscent of that in *Didelphis*, likely provided a large attachment area for muscles that served to flex, protract, abduct and adduct the limb, allowing these muscles to generate significant force (Heinrich and Rose, 1997). The very large size of this crest also brings to mind aquatic animals, such as the pinniped *Callorhinus*; we feel it is unlikley "*M.*" *uintensis* was a swimming creature, but the large size of the crest is striking. The relatively round radial head, such as found in the arboreal *Nandinia*, of AMNH 1964 indicates that the limb was commonly supinated substantially (Heinrich and Rose, 1997). All of these characteristics suggest an arboreal lifestyle, most notably the large deltopectoral crest that has been linked specifically to enhanced climbing in modern viverrid carnivorans (Taylor, 1974). However, not all morphological functional indicators of the forelimb point to an arboreal animal. The large capitular eminence of the radius, trochlea extending more distally than the capitulum, well–developed anconeal process, and deep olecranon fossa all are morphological features thought to be associated with increased stability at the elbow joint (Heinrich and Rose, 1997). This increased stability in turn is associated with a less arboreal and more scansorial or terrestrial life style, as these features, in various combinations, are seen in the living carnivorans *Ailuropoda* and *Mustela*.

The hindlimb also paints a somewhat incongruent picture of the locomotion of "*Miacis*" *uintensis*, but to a lesser extent than the forelimb. The rounded femoral head, with an articulation surface that extends slightly upon the neck, as seen in the scansorial viverrid *Paradoxurus*, is indicative of an extensive range of motion of the limb, associated with arboreality and scansoriality (Heinrich and Rose, 1997). However, the posteriorly directed lesser trochanter of the femur, as seen in herpestids, is associated with a more limited range of motion (Heinrich and Rose, 1997). The deep patellar groove may represent a capacity to rapidly flex and extend the knee (Heinrich and Rose, 1997), a feature often seen in non–arboreal taxa such as *Canis*. A large peroneal tubercle is common in modern climbing carnivorans such as *Nandinia*; in these taxa the peroneal musculature works to evert, abduct, and plantarflex the foot. In contrast, a reduced peroneal tubercle, such as occurs in AMNH 1964, implies a loss of mobility of the foot, as exhibited by cursorial terrestrial taxa (Heinrich and Rose, 1997). However, not all arboreal taxa have a large peroneal tubercle, the arboreal *Bassaricyon*, for example. Arboreal features of the calcaneus are the position of the sustentaculum distal to the astragalocalcaneal facet and the gentle curvature of this facet, as seen in aboreal taxa such as *Ailurus* and *Bassaricyon* (Polly, 2008).

As a whole, the morphology of "*Miacis*" *uintensis* suggests ambiguous functional interpretations. The taxon most likely took advantage of both arboreal and terrestrial habitats, with perhaps a greater emphasis on scansorial or terrestrial locomotion. This combination of arboreal and non–arboreal morphological indicators, is similar (but not identical) to the condition observed in *Hesperocyon* (Wang, 1993). Many of the features in *Hesperocyon* interpreted to signify a relatively cursorial mode of life can be found in AMNH 1964, such as the narrow patella trochlea and the position of the fovea capitis femoris. Conversely, features in AMNH 1964 that signify arboreality in other taxa can also be found in a less well–developed fashion in *Hesperocyon*, such as an acromion process on the scapula and a deltopectoral crest. This mosaic appearance of features thought to indicate either arboreal or terrestrial locomotor habitus (based on their occurrences in living taxa with known locomotion), and the sharp differences from the anatomical conditions and inferred locomotor styles in other "miacids," suggests a wider range of locomotor adaptations in stem early carnivoramorphans than has been presumed previously. Within the monophyletic basal Viverravidae a similar range of locomotor adaptations has been inferred, based on a slightly smaller sample size. Additionally, it implies that reconstructing locomotion in ancient taxa may be complicated by unique morphological specializations (and combinations of anatomical traits) and/or retentions of ancestral features that may not fully or accurately reflect the actual locomotor range of the fossil taxa.

PHYLOGENETIC ANALYSIS

Results

The analysis returned 9 most parsimonious trees of 454 steps each. The topology of the strict consensus tree is shown in Figure 3. Taxon names in this tree vary slightly from those published in Wesley–Hunt and Flynn (2005). The OTU formerly labeled *Prohesperocyon wilsoni* is now *Procynodictis vulpiceps*. The specimen

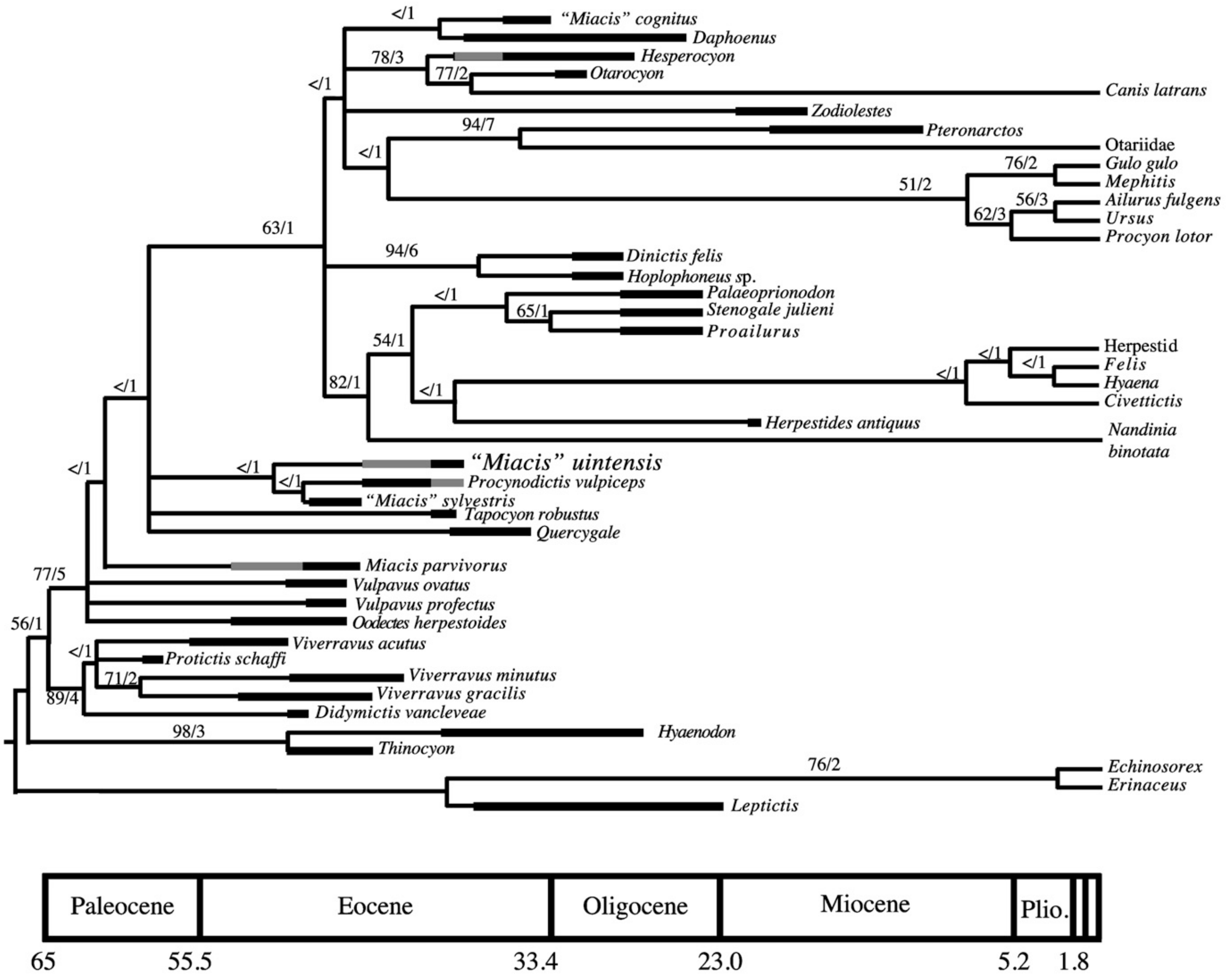

FIGURE 3. Strict consensus phylogeny of the nine most parsimonious trees of 454 steps each recovered in the phylogenic analysis. Values above or below branches represent bootstrap scores followed by Bremer decay support indices. Time ranges indicated by larger bars, if the bars are lighter the occurrence is uncertain. Time range information comes from Baskin, 1998; Berta, 1994; Flynn, 1998; Gunnell, 1998; Hunt, 1991, 1998a, 1998b; Martin, 1998; and Munthe 1998. The curve on the bottom represents relative temperatures through time, derived from isotopic data. Curve comes from Zachos et al, 2001. **Abbreviations**: **Ck**, Clarkforkian; **Du**, Duchesnean; **Or**, Orellan; and **Wt**, Whitneyan.

coded by Wesley–Hunt and Flynn (2005) for this terminal is CM 11900, the holotype of *Miacis gracilis* (Clark). This species was synonymized by Wang and Tedford (1996) with *Procynodictis vulpiceps*. The mistaken labeling from the Wesley–Hunt and Flynn (2005) publication arose due to the partial synonymy of "*M.*" *gracilis* with *Prohesperocyon wilsoni* by Wang (1994). This referral, however, did not include the species as a whole, but only fragmentary material originally published by Wilson et al. (1968). Evidence in support of this revised taxonomic assignment is the explicit referral of the skull of CM 11900 in Wang and Tedford (1994) as "*M.*" *gracilis*. Furthermore, Wang and Tedford's (1996) referral of the species to *Procynodictis vulpiceps* makes specific reference to the skull discussed in their previous paper. As both Wang and Tedford (1994, 1996) papers also mention *Prohesperocyon wilsoni* as a separate taxon, there is no doubt regarding the separation of these species in the most recent comprehensive taxonomic analyses of that material and clade.

In Figure 3, AMNH 1964 is nested among the paraphyletic array of taxa previously assigned to the "Miacidae." The present analysis places "*Miacis*" *uintensis* as nearest outgroup to the clade of *Procynodictis vulpiceps* and "*M.*" *sylvestris*. "*M.*" *uintensis* lies closer to crown Carnivora than do the two *Vulpavus* species included in this analysis. Although postcrania are reported for "*M.*" *petilus*, this taxon could not be included in the current analysis because neither the basicranium nor the upper dentition is known for the species. If it is coded only from the sparse material known, there is a dramatic loss of resolution across the entire phylogeny (as this poorly known taxon, with extensive missing character data, can be placed equally parsimoniously in many places throughout the tree). However, even the initial analyses that included this incomplete taxon indicate that "*M.*" *petilus* undoubtedly would fall among the paraphyletic array of taxa traditionally considered to be members of the "Miacidae," and it is likely it would lie outside of crown Carnivora, as do all the other putative "*Miacis*" species.

When the consensus topology of this analysis is compared to the strict consensus tree of Wesley-Hunt and Flynn (2005), relationships among the Viverravidae and the basal–most stem carnivoramorphans are identical, but higher in the tree there are several major topological differences. There is still a polytomy of the *Vulpavus* specimens and *Oödectes*, although *Tapocyon* is not found unambiguously as the closest outgroup to crown Carnivora. Instead *Tapocyon* is part of the aforementioned polytomy containing the group that includes "*M.*" *uintensis*. (AMNH 1964). *Quercygale*, which was not included in the analysis of Wesley–Hunt and Flynn (2005), is also part of this polytomy. In the study of Wesley–Hunt and Werdelin (2005), which used a more limited sampling of Caniformia, *Quercygale* was the nearest outgroup to Carnivora.

Relationships within Carnivora also differ in the present analysis, although it must be emphasized that the relatively sparse taxon sampling within Carnivora was not intended to resolve interrelationships among members of the crown group in either this study or that of Wesley–Hunt and Flynn (2005). The Nimravidae are not unambiguously placed as members of the Feliformia, as in Wesley-Hunt and Flynn (2005), but instead lie in a tritomy with Feliformia and Caniformia. There also is a loss of resolution within the Caniformia, but no novel relationships are indicated. Although the taxon and character sampling are sufficient to resolve the interrelationships of many basal carnivoramorphans, refining the interrelationships of all Carnivora and Carnivoramorpha awaits more comprehensive taxon and character sampling.

Discussion

"*Miacis*" *uintensis* is only distantly related to the type species of *Miacis*, *M. parvivorus*. While this result could be used to support the removal of "*M.*" *uintensis* from the "genus," support for relationships among the "Miacidae" as a whole are not strong, with both low bootstrap values and decay indices, and thus extensive taxonomic revisions across the entire suite of early carnivoramorphan taxa should await a more definitive analysis. Additionally many species currently placed within *Miacis* have not been able to be incorporated into this analysis. Therefore, it would be premature to definitively remove "*M.*" *uintensis* from the clade based on the genotypic species. If "*M.*" *uintensis* were now removed taxonomically from the genus, only later to be 'relumped' into the grouping, it would result in additional and possibly unnecessary taxonomic changes and confusion.

When the hypothesis of relationships of the Carnivoramorpha from this study is compared to those of previous studies (Wesley-Hunt and Flynn, 2005; Wesley–Hunt and Werdelin, 2005) there are several consistently supported relationships, including monophyletic Viverravidae as nearest outgroup to a paraphyletic array of taxa once lumped together as the "Miacidae"; that paraphyletic array forms a sequential series of nearer outgroups to crown Carnivora. Disagreement among the prior and present analyses lies in the placement of various taxa among this paraphyletic stem lineage. However, placements of some of these taxa seem to be rather firm. *Oödectes*, the *Vulpavus* species, and *Miacis parvivorus* always fall towards the base of the lineage leading to the remainder of the "Miacidae" plus crown Carnivora, whereas "*M.*" *sylvestris*, *Procynodictis vulpiceps*, *Tapocyon robustus*, and *Quercygale angustidens* always are more closely related to Carnivora than are any of those basal taxa. Additionally a small monophyletic subset of taxa previously grouped as the "Miacidae" is recovered in all published analyses, although outside of the constant linking of "*M.*" *sylvestris* and *Procynodictis vulpiceps*, its precise composition is variable. In the present analysis "*M.*" *uintensis* is the first–diverging member of this small-unnamed clade, and it is the only other taxon (beyond the clade of "*M.*" *sylvestris* and *Procynodictis vulpiceps*) found in this group in all most parsimonious trees. *T. robustus* was placed as a member of this group in the analysis of Wesley–Hunt and Werdelin (2005), but this relationship was not identified in all most parsimonious trees in the current study.

Reconstruction of Ancestral Morphological Conditions

Figure 4 shows relationships among early diverging carnivoramorphans, with reconstructed locomotor styles mapped onto the phylogeny via the parsimony algorithm in Mesquite. Included are the three "Miacidae" taxa discussed in the present paper: "*Miacis*" *petilus*, *Vulpavus*, and "*M.*" *uintensis*. As "*M.*" *petilus* could not be included in the phylogenetic analysis, its position within the clade composed of "Miacoidea" and crown Carnivora is uncertain. Also included in the current analysis are members of the Viverravidae for which detailed postcranial descriptions are available: *Viverravus acutus* (Heinrich and Houde, 2006), *Didymictis protenus* (Heinrich and Rose, 1997), and *Protictis*, which is very fragmentary and has been only tentatively interpreted with respect to its locomotor specializations (Heinrich and Houde, 2006). Interestingly, Heinrich and Houde's (2006) recent paper suggested , as this paper independently reconstructs for various "miacids," that the viverravids did not all occupy the same adaptive zone. Crown Carnivora is represented by *Hesperocyon gregarius*, a basal canid, and *Nandinia binotata*, the taxon consistently found to be the earliest diverging feliform in both morphological and molecular analyses.

Selected creodonts also are included for outgroup comparisons. Locomotor inferences for creodonts are taken from Polly (1996) and Gebo and Rose (1993). Topology of interrelationships among the Hyaenodontidae comes from Polly (1996). The two traditional groupings of creodonts, Hyaenodontidae and Oxyaenidae, are placed in a tritomy with Carnivoramorpha, to

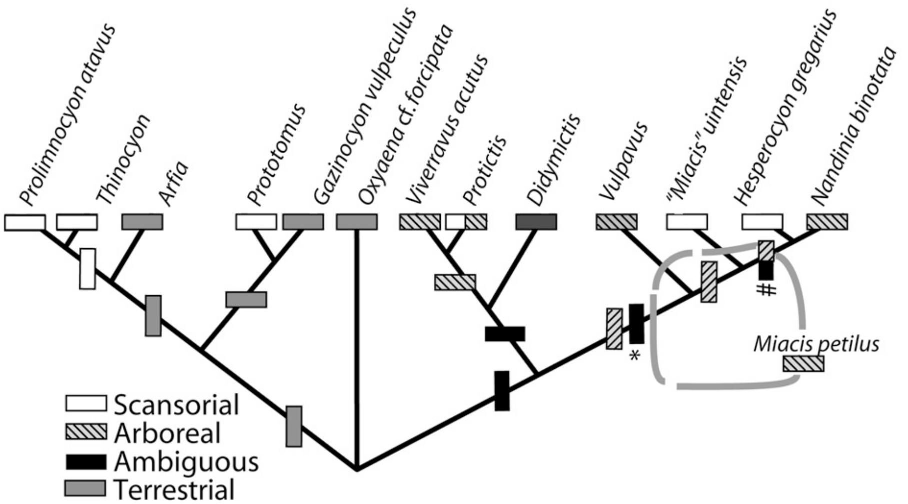

FIGURE 4. Reconstructed locomotor or styles of basal carnivoramorphans mapped onto a pruned version of the strict consensus tree, with Creodonta as outgroups. Most taxa are only identified to the generic level due to either the lack of more precise identification in the source material or lack of complete overlap between species chocen for inclusion in the phylogenic analysis and those with enough available material for functional analysis. * Ambiguous reconstruction if *"Miacis" petilus* groups with *Vulpavus*. # - Ambiguous reconstruction, unless *"Miacis" petilus* groups with *"Miacis" uintensis.*

reflect the lack of certainty of interrelationships among these clades. See Flynn and Wesley–Hunt (2005) for an elaborated discussion of creodont and carnivoramorphan relationships.

When the inferred locomotor styles are mapped onto the most parsimonious tree from the current analysis (reduced to include only the early Cenozoic carnivoramorphans for which postcranial anatomy has been analyzed in detail), the ancestral viverravid condition is ambiguous. In contrast, the last common ancestor (LCA) of all "miacids" (i.e., the LCA of "miacids" and crown Carnivora) is optimized as having arboreal ancestry for all but one possible position of the ambiguously positioned taxon "*Miacis*" *petilus*. If "*M.*" *petilus* is placed as the nearest relative of *Vulpavus*, then the ancestral condition is ambiguous. The inclusion or exclusion of the very fragmentary *Protictis* does not change the results. Ancestral state reconstructions also are not affected if scansoriality is treated as a combination of terrestrial and arboreal features, rather than as a separate state.

The sparse sample of postcrania currently available for early carnivoramorphans is a limitation. With the data available at present, the optimized ancestral habitus of Carnivoramorpha is ambiguous, as is the Viverravidae condition. The condition for the unnamed node of all Carnivoramorpha except Viverravidae is reconstructed alternatively as either arboreal or ambiguous depending on the position of "*Miacis*" *petilus*. The ancestral reconstruction of Carnivora is likewise ambiguous based upon the position of this taxon; in this case almost all positions of "*M.*" *petilus* result in an ambiguous interpretation, largely driven by the conflicting locomotor styles for the two crown Carnivora analyzed in this locomotor study.

While relatively complete postcranial skeletons of early carnivoramorphans are not common, more are present in existing museum collections than is typically perceived, and increasing numbers are being recovered from new fieldwork. Of special interest are almost complete skeletons of *Oödectes*, *Tapocyon*, and many species of *Miacis* that have not been included in this analysis, since they have not yet been prepared or studied in detail. Detailed anatomical and phylogenetic analyses of the taxa represented by these new skeletons hold great potential for more accurately reconstructing their locomotor adaptations, better constraining ancestral conditions for various clades, and enhancing understanding of the breadth and timing of diversification within the early radiation of Carnivora and their nearest relatives. However, at this time there is not enough material that both has been studied and can be placed confidently in a phylogenetic framework, thus precluding a reconstruction of the evolution of locomotor methods of early Carnivoramorpha that is more reliable and stable.

CONCLUSIONS

The postcranial skeleton of "*Miacis*" *uintensis* (AMNH 1964) described here differs in many ways from that of previously described "miacids." The majority of anatomical differences have been associated with a predominantly non–arboreal locomotor habit in living Carnivora (Taylor, 1974, 1976). These features include a deep olecranon fossa, large capitular eminence on the radius, posteriorly projecting lesser trochanter, narrow and deep patella trochlea surface, and reduced peroneal tubercle on the calcaneus. This reconstructed locomotor mode contrasts with the fully arboreal habit previously attributed to "miacids" such as *Vulpavus* and *Miacis* (Heinrich and Rose, 1995 and 1997, and Rose, 1990). In contrast to this series of traits indicating terrestriality, some features of "*M.*" *uintensis* suggest arboreality, such as the high deltopectoral crest on the humerus, large supinator crest, low greater tubercle, flat radial notch, round radial head, femoral head with an expanded articulation surface, and the relatively flat astragalar trochlea (Taylor, 1974). The resolution of the phylogenetic position of this taxon in the current study is essential for better understanding of the acquisition of this unique mix of features thought to indicate alternative interpretations of locomotor specialization, and indicate a locomotor style not previously observed in any other basal carnivoramorphan.

Interpretation of the postcranial morphology of "*Miacis*" *uintensis* (AMNH 1964) also bears on prior reconstructions of locomotor evolution in *Hesperocyon* and canids (Wang, 1993). Wang (1993) suggested that *Hesperocyon* represented a "transitional state" between arboreal "miacids" (which were at that time interpreted to be homogeneous in their locomotor style, and more closely related to caniforms than feliforms) and cursorial canids. However, it now is clear that the transition from an arboreal habitus to a scansorial or terrestrial life in the canid lineage did not necessarily begin within the evolution of the canid carnivorans, but possibly began earlier, prior to the split of the Caniformia (including canids) and Feliformia, within the paraphyletic stem lineage of early carnivoramorphans. More detailed and comprehensive analyses including postcranial characteristics for a broader range of early Cenozoic taxa must be conducted to determine how many times and when evolution of a terrestrial habitus evolved within the Carnivoramorpha. Specifically, the placement of "*M.*" *uintensis* as the earliest diverging member of a unnamed possibly monophyletic subset of taxa that formerly were part of the "Miacidae" is intriguing. However, further examination of basal carnivoramorphan postcranial anatomy is necessary before it can be determined if, among the various taxa traditionally assigned to the "Miacidae," a relatively high degree of terrestrial adaptation is confined to this possible group or more widespread across early carnivoramorphans.

One interesting correlation at present is the temporal restriction of the arboreal "miacids" to the early Eocene, with the more terrestrial "*M.*" *uintensis* occurring far later in the Eocene. The early Eocene was a very warm period in Earth's history (Wing et al, 2005), quickly followed by a cooling trend. The vegetation of this period rapidly changed as well, with a notable decrease in forest cover in western North America as the climate cooled (Wing, 1998; Wing et al., 2005). It is tempting to state that the shift of "miacids" from arboreal to a more scansorial mode of life was triggered by this change in vegetation patterns due to the cooling events. However, our sample size at this point in time is admittedly small, and this rough correlation will need to be subjected to much more rigorous testing before we can firmly associate the global temperature changes with a change in basal carnivoramorphan locomotion.

The results of the new analysis of the postcrania and phylogenetic relationships of "*Miacis*" *uintensis* clearly indicate that the current view of the "miacids" as predominantly arboreal animals needs to be broadened substantially to accommodate a more diverse suite of locomotor styles for taxa during the early diversification of Carnivoramorpha. As could be expected in a paraphyletic series of stem taxa, "miacids" varied greatly in size and morphology, reflecting differing locomotor and ecological adaptations, and unique mosaic combinations of retention of ancestral, primitive features and apomorphic specializations. No single taxon can be viewed as representative of ancestral conditions for such a diverse suite of organisms representing the initial diversification of the Carnivoramorpha.

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LITERATURE CITED

Baskin, J. A. 1998. Mustelidae pp 152–173 in C. M. Janis, K. M. Scott, and L. L. Jacobs (eds.), Evolution of Tertiary Mammals of North America. Volume 1. Terrestrial Carnivores, Ungulates, and Ungulate-like Mammals. Cambridge University Press, Cambridge.

Berta, A. 1994. New specimens of the pinnipediform *Pteronarctos* from the Miocene of Oregon. Smithsonian Contributions to Paleobiology. 78:1–30.

Bryant, H. N. 1991. Phylogenetic relationships and systematics of the Nimravidae (Carnivora). Journal of Mammalogy 72:56–78.

Bryant, H. N. 1992. The Carnivora of the Lac Pelletier Lower Fauna Eocene: Duchesnean, Cypress Hills Formation, Saskatchewan. Journal of Paleontology 66:847–855.

Flynn, J. J., and H. Galiano. 1982. Phylogeny of early Tertiary Carnivora, with a description of a new species of *Protictis* from the middle Eocene of northwestern Wyoming. American Museum Novitates 2725:1–64.

Flynn, J. J. 1988. Early Cenozoic Carnivora ("Miacoidea"); pp. 110–123 in C. M. Janis, K. M. Scott, and L. L. Jacobs (eds.), Evolution of Tertiary Mammals of North America. Volume 1. Terrestrial Carnivores, Ungulates, and Ungulatelike Mammals. Cambridge University Press, Cambridge.

Flynn, J. J., and G. D. Wesley−Hunt. 2005. Carnivora; pp 175–198 in K. Rose and D. Archibald (eds.), The Rise of Placental Mammals: Origins and Relationships of the Major Extant Clades. Johns Hopkins University Press, Baltimore.

Gebo, D. L., and K. D. Rose. 1993. Skeletal morphology and locomotor adaptation in *Prolimnocyon atavus*, an early Eocene hyaenodontid creodont. Journal of Vertebrate Paleontology. 131:125–144.

Gingerich, P. D. 1983. Systematics of early Eocene Miacidae (Mammalia, Carnivora) in the Clark's Fork Basin, Wyoming. Contributions from the Museum of Paleontology, University of Michigan 27:87–128.

Gunnell, G. F. 1998. Creodonta; pp. 91–109 in C. M. Janis, K. M. Scott, and L. L. Jacobs (eds.), Evolution of Tertiary Mammals of North America. Volume 1. Terrestrial Carnivores, Ungulates, and Ungulatelike Mammals. Cambridge University Press, Cambridge.

Heinrich, R. E., and P. Houde. 2006. Postcranial anatomy of *Viverravus* (Mammalia, Carnivora) and implications for substrate use in basal Carnivora. Journal of Vertebrate Paleontology 262:422–435.

Heinrich, R. E., and K. D. Rose. 1995. Partial skeleton of the primitive carnivoran *Miacis petilus* from the early Eocene of Wyoming. Journal of Mammalogy 761:148–162.

Heinrich, R. E., and K. D. Rose. 1997. Postcranial morphology and locomotor behavior of two early Eocene miacoid carnivorans, *Vulpavus* and *Didymictis*. Palaeontology 402:279–305.

Hunt, R. M. 1991. Evolution of the aeluroid Carnivora: Viverrid affinities of the Miocene carnivoran *Herpestides*. American Museum Novitates 3023:1–34.

Hunt, R. M. 1998a. Evolution of the aeluroid Carnivora: Diversity of the earliest aeluroids from Eurasia (Quercy, Hsanda–Gol) and the origin of felids. American Museum Novitates 3252:1–65.

Hunt, R. M. 1998b. Amphicyonidae, pp 196–227 in C. M. Janis, K. M. Scott, and L. L. Jacobs (eds.), Evolution of Tertiary Mammals of North America. Volume 1. Terrestrial Carnivores, Ungulates, and Ungulatelike Mammals. Cambridge University Press, Cambridge.

Janis, C. M., J. A. Baskin, A. Berta, J. J. Flynn, G. F. Gunnell, R. M. Hunt, Jr., L. D. Martin, K. Munthe, 1998. Carnivorous mammals. *In:* Evolution of Tertiary mammals of North America, Volume 1: Terrestrial Carnivores, Ungulates, and Ungulatelike Mammals, ed. C. M. Janis, K. M. Scott, and L. L. Jacobs, New York, Cambridge University Press:73–94.

Jenkins, F. A. J. 1974. The movement of the shoulder in claviculate and aclaviculate mammals. Journal of Morphology 144:71–84.

Legendre, S., and C. Roth. 1988. Correlation of carnassial tooth size and body weight in recent carnivores. Historical Biology 1:85–98.

Maddison, W. P., and D. R. Maddison. 2007. Mesquite: a modular system for evolutionary analsysis. Verison 2.01 http://mesquiteproject.org.

Martin, L. D. 1998. Nimravidae. Pp. 228–235 in C. M. Janis, K. M. Scott, and L. L. Jacobs (eds.), Evolution of Tertiary Mammals of North America. Volume 1. Terrestrial Carnivores, Ungulates, and Ungulatelike Mammals. Cambridge University Press, Cambridge.

Matthew, W. D. 1909. The Carnivora and Insectivora of the Bridger Basin, middle Eocene. Memoirs of the American Museum of Natural History 9:289–567.

Munthe, K. 1998. Canidae, pp 124–134 in C. M. Janis, K. M. Scott, and L. L. Jacobs (eds.), Evolution of Tertiary Mammals of North America. Volume 1. Terrestrial Carnivores, Ungulates, and Ungulatelike Mammals. Cambridge University Press, Cambridge.

Osborn, H. F. 1985. Fossil Mammals of the Uinta Basin. Bulletin of the American Museum of Natural History 7:71–105.

Polly, P. D., G. D. Wesley–Hunt, R. E. Heinrich, G. Davis, and P. Houde. 2006. Earliest known carnivoran auditory bulla and support for a recent origin of crown–group Carnivora (Eutheria, Mammalia). Palaeontology 49:1019–1027.

Polly, P. D. 2008. Adaptive Zones and the Pinniped Ankle:A 3D Quantitative Analysis of Carnivoran Tarsal Evolution. Pp. 165–194 (E. Sargis and, M. Dagosto,, Eds), Mammalian Evolutionary Morphology: A Tribute to Frederick S. Szalay. Springer:Dordrecht, The Netherlands.

Rose, K. D. 1990. Postcranial skeleton remains and adaptations in early Eocene mammals from the Willwood Formation, Bighorn Basin, Wyoming; pp 107–134 In T. M. Bown and K. D. Rose (eds) Dawn of the Age of Mammals in the northern part of the Rocky Mountain Interior of North America, Special paper / Geological Society of America 243:1–241.

Sorenson, M. D. 1999. TreeRot, version 2. Boston, MA, Boston University.

Swofford, D. L. 2000. PAUP*. Phylogenetic analysis using parsimony and other methods Version 4.0. Sunderland, MA, Sinauer Associates.

Taylor, M. E. 1974. The functional anatomy of the forelimb of some African Viverridae Carnivora. Journal of Morphology 1433: 307–336.

Taylor, M. E. 1976. The functional anatomy of the hindlimb of some African Viverridae Carnivora. Journal of Morphology 1482: 227–254.

Wang, X. 1993. Transformation from plantigrady to digitigrady: functional morphology of locomotion in *Hesperocyon* Canidae: Carnivora. American Museum Novitates 3069:1–23.

Wang, X. 1994. Phylogenetic systematics of the Hesperocyoninae Carnivora: Canidae. Bulletin of the American Museum of Natural History 221:1–207.

Wang, X., and R. H. Tedford. 1996. Canidae pp. 646–664 in D. R. Prothero and R. J. Emry (eds.), The Terrestrial Eocene–Oligocene Transition in North America. Cambridge Univ. Press, Cambridge.

Wesley, G. D., and J. J. Flynn. 2003. A revision of *Tapocyon*, including analysis of the first cranial specimens, identification of a new species, and implications for the phylogeny of basal Carnivora. Journal of Paleontology 77:769–783.

Wesley–Hunt, G. D., and J. J. Flynn. 2005. Phylogeny of the Carnivora: basal relationships among the carnivoramorphans, and assessment of the position of ‘Miacoidea’ relative to Carnivora. Journal of Systematic Palaeontology 31:1–28.

Wesley–Hunt, G. D., and L. Werdelin. 2005. Basicranial morphology and phylogenetic position of the upper Eocene carnivoramorphan *Quercygale*. Acta Palaeontologica Polonica 504:837–846.

Wing, S. L. 1998. Tertiary vegetation of North America as a context for mammalian evolution. Pp 37–65 in C. M. Janis, K. M. Scott, and L. L. Jacobs (eds.), Evolution of Tertiary Mammals of North America. Volume 1. Terrestrial Carnivores, Ungulates, and Ungulatelike Mammals. Cambridge University Press, Cambridge.

Wing, S. L., G. J. Harrington, F. Smith, J. I. Bloch, and D. M. Boyer. 2005. Transient floral change and rapid global warming at the Paleocene–Eocene boundary. Science 310:993–996.

Wortman, J. L., and W. D. Matthew. 1899. The ancestry of certain members of the Canidae, the Viverridae, and Procyonidae. Bulletin of the American Museum of Natural History 12:109–138.

Wyss, A. R., and J. J. Flynn. 1993. A phylogenetic analysis and definition of the Carnivora. pp 32–52 in F. S. Szalay, M. J. Novacek, and M. C. McKenna (eds.), Mammal phylogeny: placentals. Volume 2, New York: Springer–Verlag.

Zachos, J., M. Pagani, L. Sloan, E. Thomas, and K. Billups. 2001. Trends, rhythms, and aberrations in global climate 65ma to Present. Science 292:686–693.

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