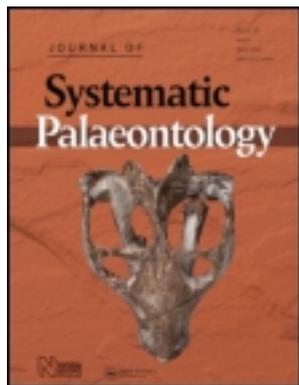


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## Phylogeny of the Carnivoramorpha: The impact of postcranial characters

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Previous analyses of the mammalian clade Carnivoramorpha have tended to sample only cranial and dental character systems, particularly those that included early Cenozoic taxa, Viverravidae and basal Carnivoraformes (the latter being a paraphyletic array of taxa traditionally referred to as the ‘Miacidae’). In this study we add more than 100 postcranial characters to an existing dataset dominated by cranio-dental characters. The addition of the new characters permits the inclusion of a large number of basal carnivoraforms, known solely or predominantly from postcranial characters, that previously would have been ‘unplaceable’ in a phylogenetic analysis. The resultant phylogeny recovers most of the same clades identified in previous studies, but resolves some relationships differently within the basal carnivoraforms. A novel (unnamed) monophyletic subclade of the Carnivoraformes is recovered, supported in part by characters from both the prior and new datasets. The inclusion of a substantial suite of postcranial characters expands the ability to assess the relationships of basal carnivoramorphans taxa, and permits the inclusion of many taxa represented only by incomplete material.

**Keywords:** Carnivoramorpha; Carnivora; postcrania; Eocene; Carnivoraformes; Viverravidae

### Introduction

Carnivoramorph phylogeny has been the focus of a number of recent morphological cladistic studies (e.g. Wyss & Flynn 1993; Wesley-Hunt & Flynn 2005). Those attempts to reconstruct relationships of taxa within this clade relied primarily upon cranial and dental characters, to near total exclusion of the postcranial skeleton (only five postcranial characters were included in both cited studies). Postcranial characters could be an important source of phylogenetic information, however, as they also should reflect synapomorphies due to shared ancestry. Serious undersampling of postcranial characters in carnivoramorph phylogeny is especially striking in light of several studies of other mammalian orders that include substantial data from the postcranium, such as for Primates (Bloch *et al.* 2007), Artiodactyla (including cetaceans; Spaulding *et al.* 2009) and Pholidota (Gaudin *et al.* 2009). Potential explanations for this lack of inclusion are the difficulty of associating postcrania and craniodental elements in disarticulated specimens, and longstanding assumptions (untested) that the skeleton of early carnivoramorphans resembled a presumed generalized placental condition and many specializations observed reflected function (such as locomotion) rather than phylogeny. On this latter point, Sanchez-Villagra & Williams (1998) examined a large number of datasets for

mammals, seeking to determine if there was a significantly different level of homoplasy in cranial, dental or postcranial character sets. They found, measured by the consistency index, that there was no statistically significant difference in the resolving power of characters from any of these arbitrary partitions. In addition, studies with a functional morphology emphasis (e.g. Sargis 2002; Young 2008) have routinely found that the impact of phylogeny cannot be discounted when examining postcranial adaptations.

Several previous studies particularly sought to clarify the relationships between carnivoramorph taxa from the Palaeocene and Eocene and crown clade Carnivora (e.g. Flynn & Galiano 1982; Flynn *et al.* 1988; Wyss & Flynn 1993; Wesley-Hunt & Flynn 2005 – see this latter paper for an in-depth review of prior studies). These early Cenozoic fossil taxa generally have been reconstructed to be either members of the monophyletic clade Viverravidae or basal Carnivoraformes (Carnivoraformes name following Flynn *et al.* 2010). The Viverravidae are known from the early Palaeocene to late Eocene, and have been firmly established as a monophyletic clade that is the nearest outgroup to the rest of the Carnivoramorpha (Wesley-Hunt & Flynn 2005; Spaulding & Flynn 2009). Basal Carnivoraformes are known from the late Palaeocene to late Eocene. This array of early carnivoraform taxa, previously referred to as the ‘Miacidae’, has been documented to be paraphyletic

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in a number of the studies cited above, and their potential monophyly was firmly refuted in the latest comprehensive morphological phylogeny (Wesley-Hunt & Flynn 2005). However, a recent cladistic study of this diverse suite of basal Carnivoraformes has shown that our ability to resolve their interrelationships is limited in the absence of postcranial characters (Spaulding & Flynn 2009). When the topology derived from the character matrix of Wesley-Hunt & Flynn (2005; emphasizing basicranial and dental characters) is compared with subsequent studies (e.g. Wesley-Hunt & Werdelin 2005; Polly *et al.* 2006) using a similar character set but incorporating additional taxa with relatively complete dental and basicranial material, there is little if any change in topology from the earlier analysis. However, when additional taxa lacking complete dental and basicranial material, such as “*Miacis*” *uintensis* (Spaulding & Flynn 2009) and *Dawsonicyon isami* (Spaulding *et al.* 2010), are added to the analysis, the topology among basal taxa becomes more poorly resolved and less stable, indicated by an increase in the number of polytomies and reduced nodal support. In an attempt to resolve this instability issue, generate better-resolved topologies and increase nodal support, we incorporate all available morphological information in a single analysis, particularly by adding extensive but previously unsampled information from the postcranial skeleton and including additional taxa.

The postcranial skeleton has not been well studied for many basal carnivoraform taxa, with detailed descriptive and comparative work being even more limited (Matthew 1909; Clark 1939; Heinrich & Rose 1995, 1997; Heinrich & Houde 2006; Spaulding & Flynn 2009). Few attempts have been made to use this material to develop hypotheses of relationships, outside of the works of Matthew (1909), Clark (1939) and briefly in Flynn & Galiano (1982). As noted above, the lack of attention paid to the postcranial skeleton of basal carnivoramorphans in a phylogenetic context has been due to a number of factors, including the perceived lack of material for relevant taxa (Wang & Tedford 1994) and the notion that homoplasy will be more pervasive in this character system than in cranial or dental subsets (Turner 1848; Flower 1869). While fossil taxa are more commonly known from teeth than from other skeletal elements, a substantial amount of postcranial material is known, comparable in abundance to basicranial material. The basicranium of the skull has been considered phylogenetically informative in prior studies of the Carnivoramorpha, beginning with the pioneering work of Flower (1869), although more recent studies have shown that basicranial characters and dental features are similar in their phylogenetic informativeness (Wesley-Hunt & Flynn 2005). Of the 13 basal carnivoramorphans now incorporated in the source matrix of Wesley-Hunt & Flynn (2005) as in Spaulding *et al.* (2010), eight provide information about both basicranial and postcranial morphology, six are

associated with no postcranial material, and one preserves little if any basicranium.

In this study we demonstrate the utility of postcranial characters in resolving relationships among the Carnivoramorpha. To accomplish this goal, a postcranial data matrix was constructed and combined with the most comprehensive existing craniodental matrix (Wesley-Hunt & Flynn 2005). All taxa previously included in the craniodental matrix analyses were included, and other taxa represented by scant basicranial material were added. Several analyses of this combined matrix were then performed, each utilizing different character subsets and sets of taxa. Inclusion of postcranial characters in the combined matrix not only serves to provide more character information for taxa already included in prior analyses, thus providing an additional test of previously proposed hypotheses of relationships, but also permits the expansion of taxon sampling. This substantially enhanced sampling of characters and taxa, in turn, should give us the ability to erect more comprehensive hypotheses of the origin, diversification and evolution of the Carnivoramorpha.

## Materials and methods

The 99 character matrix of Wesley-Hunt & Flynn (2005), drawn principally from the cranium and dentition with very limited soft anatomy and postcranial features, provided the base matrix for this study. Additional postcranial characters were obtained by surveying existing systematic and descriptive literature of carnivoramorphan postcranial anatomy, and from personal observations of numerous specimens. This yielded 117 postcranial characters, 105 of which have never been utilized in a cladistic context (47 of these are derived from alpha taxonomic and descriptive literature, and the remaining 58 are from personal observations) while 12 were utilized in prior phylogenetic analyses. Taxa sampled included all those from Wesley-Hunt & Flynn (2005), taxa added to the matrix in subsequent papers (*Quercygale*, Wesley-Hunt & Werdelin 2005), *Viverravus acutus* (Polly *et al.* 2006), “*Miacis*” *uintensis* (Spaulding & Flynn 2009) and *Dawsonicyon isami* (Spaulding *et al.* 2010), and several other taxa represented by significant postcranial but little cranial material (*Didymictis protenus*, *Miacis petilus*, *Miacis washakius*, *Vulpavus palustris*, *Miacis exiguus*, *Miacis medius* and taxon indet. PM 3868, which is represented by a specimen number only as this specimen lacks any dental information and as such cannot be confidently assigned to any previously established taxon). In total, nine feliform Carnivora (five extant, four extinct), 13 caniform Carnivora (seven extant, six extinct), two nimravids (Carnivoramorpha *incertae sedis*), 16 basal Carnivoraformes and six viverravids (basal Carnivoramorpha) were included in the current analysis. Outgroup taxa were retained from prior analyses, accepting Wesley-Hunt

& Flynn's (2005) logic behind their selection, consisting of two hyaenodont creodonts, two erinaceid eulipotyphlans and the leptictid *Leptictis*.

All newly added taxa were coded from direct observations of specimens, with the exception of *Viverravus acutus*, which was coded from illustrations and descriptions of Heinrich & Houde (2006), and *Pteronarctos goedertae*, coded from descriptions in Berta (1994). Specimens examined are housed in the American Museum of Natural History, The Field Museum, The Carnegie Museum of Natural History, Yale Peabody Museum of Natural History and the Johns Hopkins segment of the US Geological Survey collections. All basal carnivoramorph OTUs were coded for the same specimen that was analysed by Wesley-Hunt & Flynn (2005). Due to dependency issues with the character originally number 44 (parastyle extends beyond metastyle) the problematic 'metastyle extends beyond the parastyle' character, original number 43, was not included in any analyses as was done for Spaulding & Flynn (2009), and here we have retained the character for compatibility of the Wesley-Hunt & Flynn partition with previous studies. When coding both outgroup and crown clade carnivoran taxa, great care was taken to ensure that the same species as in the Wesley-Hunt & Flynn analysis were utilized whenever possible. Some extant taxa, however, were coded from several species within the same genus in the Wesley-Hunt & Flynn (2005) source matrix; in those few cases, only one species per extant genus was included in the current study to minimize composite generic OTUs.

Our complete matrix contained 51 taxa coded for 216 morphological characters (available at MorphoBank, www.morphobank.org, as project 367). We analysed these in a variety of ways, to more fully explore the phylogenetic signal in these data and determine the impact and utility of incorporating the newly added postcranial characters. We first analysed the matrix including all characters and all taxa, and then the postcranial and craniodental characters were analysed separately to explore the impact of adding the postcranial characters relative to prior analyses dominated by craniodental characters. The effect of newly added taxa was examined by running the matrix with all characters included, with sequential removal and re-addition of taxa.

All character and taxa sampling exploration was conducted using the same series of search parameters. The trees were all rooted utilizing *Leptictis* as the most basal outgroup, as in the original analysis of Wesley-Hunt & Flynn (2005; see also Spaulding & Flynn 2009). The matrix was analysed in TNT version 1.1 (Goloboff *et al.* 2004). The search strategy employed in TNT was to first analyse the data under the 'New Technology search' option, selecting the sectorial search, ratchet and tree fusing search methods, all with default parameters. Under these settings, replications were run until the minimum length tree was found in 500 separate replicates, with the objective of encountering all possible tree islands. The generated trees were

then analysed under typical search options (using TBR) to fully explore the discovered tree islands. Bremer support indices were determined using TNT. Bootstrap values were calculated using PAUP\* version 4.0b (Swofford 2002), with 1000 bootstrap replicates and 10 internal trials each.

Results were examined using strict consensus, Adams consensus (Adams 1986) and agreement subtrees; in the agreement subtrees consensus method mobile taxa are pruned from the trees, showing the stable network of relationships found in all trees.

## Results

The analysis including all taxa and all characters yielded eight most parsimonious trees, each of 990 steps (Fig. 1 shows their strict consensus). Ferae, Carnivoramorpha, Carnivoraformes and Carnivora all were recovered as monophyletic clades. Within Carnivoramorpha the Viverravidae, a monophyletic group supported by seven unambiguous synapomorphies, are the nearest outgroup to all other carnivoramorphans. Relationships of taxa within Viverravidae also generally were well resolved, although the two *Didymictis* species do not group together, but instead form a basal trichotomy with the rest of the clade, possibly owing to the small amount of overlap in coding for these taxa, due to the lack of preserved morphology between these two taxa; *D. protenus* is known only from dentition and postcrania, while *D. vanclvaea* is represented exclusively by dentition and cranial features. To determine if element preservation affected the analyses, a separate analysis was undertaken in which these two species were combined into a single OTU ("*Didymictis*"); this produced no change in the remaining tree topology, so we retain the two taxa as separate OTUs in all other analyses. *Protictis schaffi* falls inside the *Viverravus* clade, offering support for the referral of this species to *Viverravus* (Polly 1997). However, we conservatively retain its original taxonomic designation, pending a comprehensive analysis focused on the Viverravidae and including more dental features traditionally used to distinguish taxa within this clade.

Carnivoraformes is supported by seven unambiguous synapomorphies. The largest polytomy in the topology is found at the base of this clade, with *Miacis washakius*, *Miacis exiguus*, *Miacis medius* and PM 3868 falling in an unresolved polytomy with a clade that includes seven other taxa of basal carnivoraforms. However, when an Adams consensus of the trees is generated (Fig. 2A), we find that the source of most of this ambiguity and lack of resolution is the three most incomplete taxa: *Miacis exiguus*, *Miacis medius* and PM 3868. Fig. 2B, the agreement subtree, shows that when those three taxa are pruned from all individual most parsimonious trees (but retained during the analysis of the matrix), this polytomy is resolved, with *Miacis washakius* as the first diverging member of the subclade of

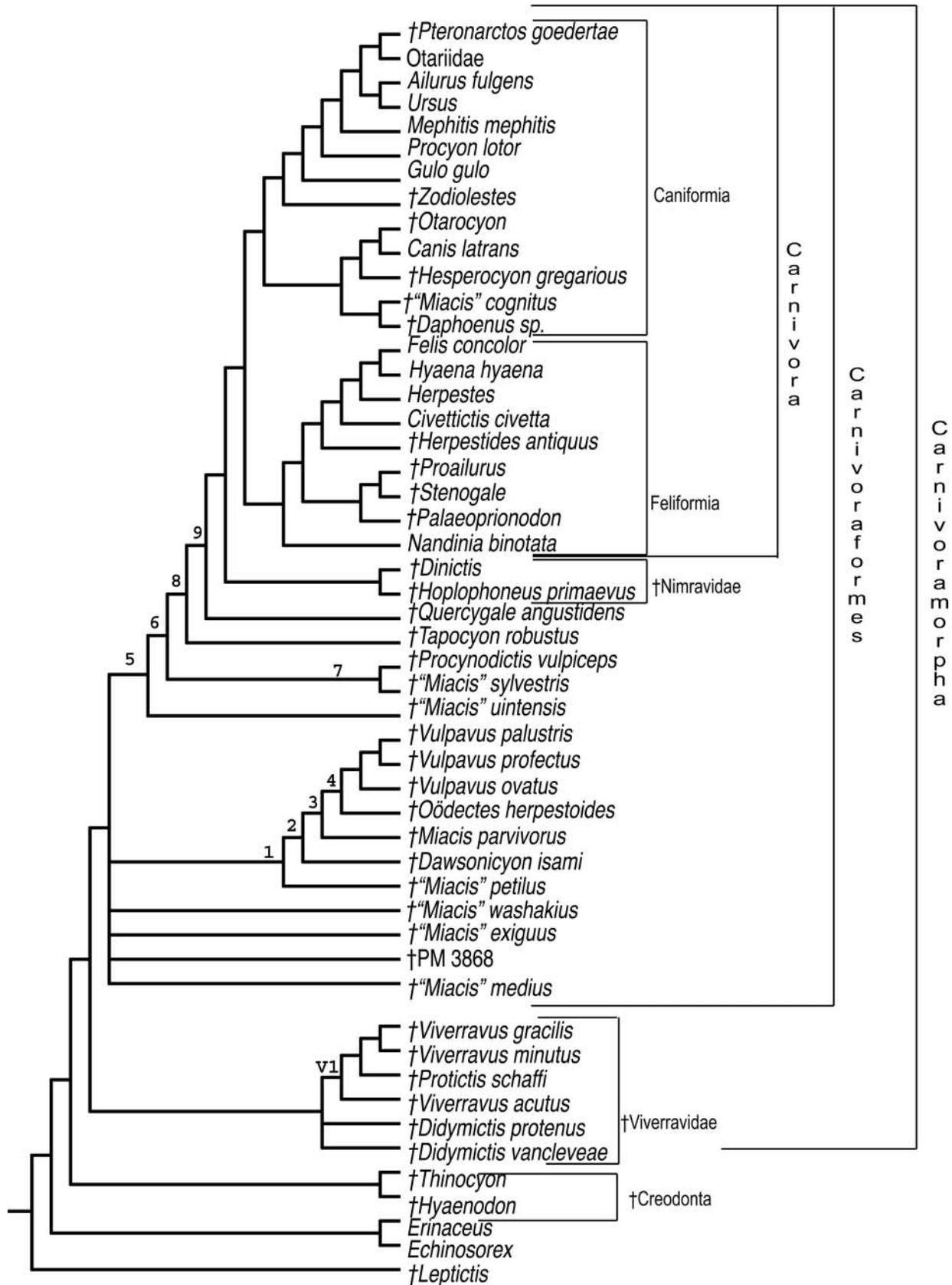
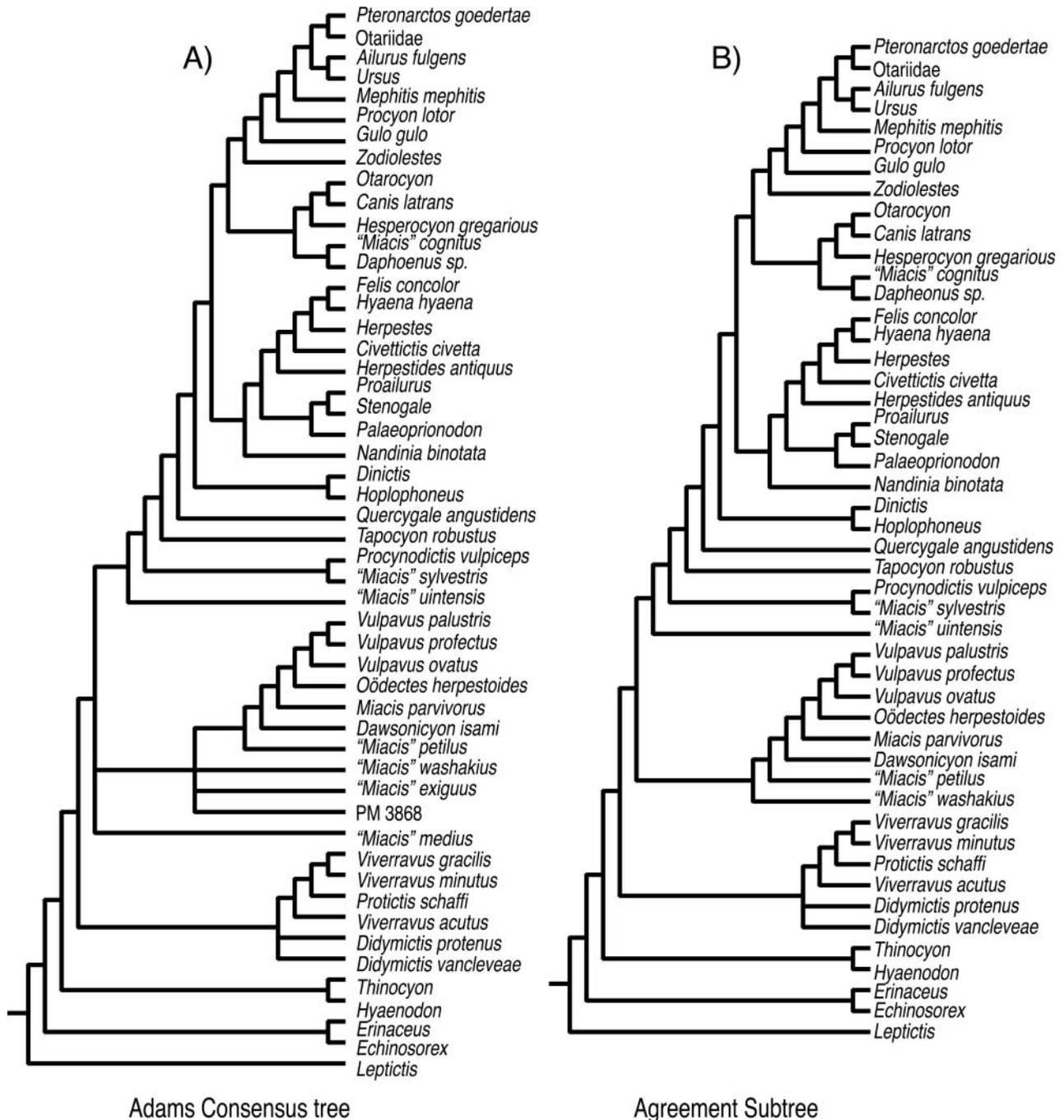


Figure 1. Strict consensus tree of the eight most parsimonious trees, of 990 steps each.



**Figure 2.** Alternative consensus trees of the eight most parsimonious trees, of 990 steps each: **A**, Adams consensus; **B**, Agreement subtree.

seven other taxa (node 1 in Fig. 1). The Adams consensus tree (Fig. 2A) resolves *Miacis medius* as possibly the first diverging species among all Carnivoramorpha. We present our results with all taxa included, as we think that a robust reconstruction of carnivoramorph phylogeny will benefit from the most complete dataset available, rather than from evaluating only selected subsets. In test runs, in which these mobile taxa were not included at all, we observed a lack

of resolution deeper within Carnivoramorpha. This demonstrates that even if we cannot refine the precise position of these taxa, they still are extremely important for providing polarities of characters and thus for better resolving interrelationships at the base of Carnivoramorpha.

Within the basal carnivoramorphs a monophyletic clade of seven taxa – node 1 in Fig. 1 – is consistently identified in the shortest trees. These taxa include all three *Vulpavus* species,

*Oödictes herpestoides*, *Miacis parvivorus* (the type species of *Miacis*), *Dawsonicyon isami* and *Miacis petilus*. We note that the type species does not group with any other species previously assigned to *Miacis* in these analyses. Crownward of the basal polytomy containing this monophyletic subset, we reconstruct a serial arrangement of the remaining taxa previously grouped in the “Miacidae” relative to crown clade Carnivora: *Miacis uintensis*, then the clade of *Miacis sylvestris* plus *Procyonictis vulpiceps*, followed by *Tapocyon robustus* then *Quercygone*. The final group that we identify outside the crown Carnivora as its most proximate outgroup is the two nimravine Nimravidae included in this analysis, *Hoplophoenus* and *Dinictis*, a clade supported by 18 synapomorphies.

Within the crown clade Carnivora (supported by 10 unambiguous synapomorphies) we recover the basal split between Caniformia (15 unambiguous synapomorphies) and Feliformia (14 unambiguous synapomorphies). Within the Caniformia clade, Canidae group with the only amphicyonid taxa analysed – *Daphoenus* and *Miacis cognitus*. Within Canidae we reconstruct the traditional arrangement of *Hesperocyon* as nearest outgroup to all other members of the clade, with Caninae and Borophaginae as sister taxa. Within the Arctoidea, *Zodiastes* is the earliest diverging branch, followed by *Gulo*. Next is *Procyon*, followed by *Mephitis*, with *Ursus* plus *Ailurus* as sister to the pinnipeds, *Pteronarcos* and Otariidae.

Within Feliformia we recovered *Nandinia* as the nearest outgroup to all other living feliforms, then three of the four fossil feliforms included in this analysis form a clade, followed by a grouping of *Herpestides antiquus* as nearest outgroup to the remaining living feliforms. Among living feliforms (besides *Nandinia*), *Civettictis* (Viverridae s.s.) is the first diverging taxon, followed by *Herpestes* (Herpestidae), and then a clade of *Felis* and *Hyaena* (Felidae and Hyaenidae, respectively), *contra* to most recent molecular analyses (e.g. Yoder *et al.* 2003; Flynn *et al.* 2005). However, when relationships of crown taxa are constrained to follow that of Flynn *et al.* (2005) no change is seen among taxa outside of crown Carnivora.

When we remove all newly added postcranial characters from this analysis (and thus also the OTU PM 3868, as it is not represented by any craniodental characters), 904 trees of 463 steps result, the strict consensus of which is presented in Fig. 3A. There is a dramatic loss of resolution in this tree relative to that including all data and all taxa. While Ferae, Carnivoramorpha and Carnivoraformes all are recovered, Carnivora is not indicated as monophyletic. Further, there is no resolution of taxa within the basal Carnivoraformes, as we only recover Arctoidea and Feliformia, but no other groupings. In this topology nimravids are included in the Feliformia rather than outside the Carnivora.

In an analysis excluding all cranial characters, and all taxa represented only by specimens preserving craniodental characters, we observe the tree topology in Fig. 3B. This

strict consensus of 173 trees, each of 516 steps, reconstructs a monophyletic Creodonta, but not Ferae or Carnivoramorpha, as the two included erinaceomorph outgroups fall between the Viverridae and the Carnivoraformes. Within Carnivoraformes we recover only the monophyletic clades Arctoidea and Nimravidae, and very little else. The majority of the remaining taxa of basal carnivoraforms, Feliformia and Canidae occur in a large unresolved polytomy. The few sub-groupings in this array are: all the species of *Vulpavus*, *Hyaena* allied with *Canis*, *Civettictis* as sister group to this pairing and the non-*Canis* canids clustering together.

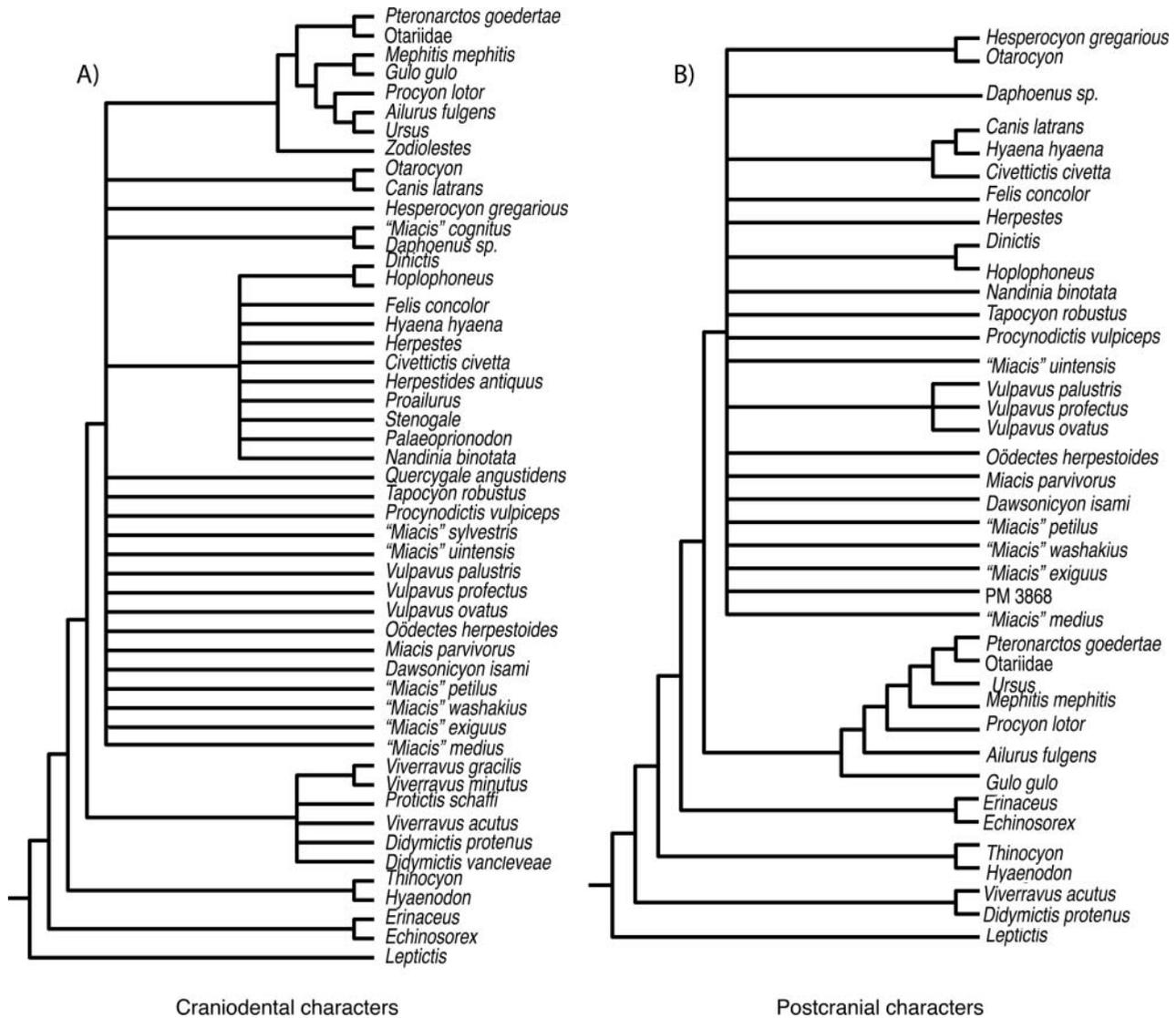
In ‘manual jack-knifing’ tests, involving the sequential removal and re-addition of taxa, no clear pattern was seen relating to the removal of each individual basal carnivoraform taxon. Typically, if one of the basal carnivoraforms was removed from the analysis, a different strict consensus tree was generated, indicating that the overall topology is highly sensitive to taxon sampling in this analysis. The most common change in resultant tree topology was a loss of resolution, not just within the basal taxa, but within the crown Carnivora as well.

Fig. 4 shows the amount of missing data within each subset of characters. While the dental character subset has less missing data than the other two, the cranial and postcranial subsets have roughly equal representation for the features represented by characters in the matrix. The exception to this is within the Viverridae, which have relatively less postcranial material known than other basal Carnivoramorpha.

## Discussion

Addition of substantial postcranial data to the matrix in this study resulted in some differences in the topology of carnivoraform relationships relative to previous studies based principally on craniodental data. Fig. 5 compares the results of the present study with those of Spaulding *et al.* (2010), the prior study with the most comprehensive sampling of morphological characters (predominantly craniodental) and early carnivoraform taxa. Broad scale relationships between the two trees are consistent – both recover Ferae, Carnivoramorpha, Carnivoraformes, Carnivora, Feliformia and Caniformia. There are marked differences, however, in the finer scale interrelationships of some taxa within these groups, particularly at the base of the carnivoraforms.

Relationships within the Viverridae are better resolved in the present analysis, contrasting with a polytomy at the base of the *Viverravus* plus *Protictis* clade in the Spaulding *et al.* (2010) craniodental analysis. The utility of or problems with adding characters, particularly those that also introduce a large amount of missing data, has been addressed previously (e.g. Wiens 1998, 2006). Here both craniodental and postcranial characters unite the Viverridae, confirming the ability of additional character data to



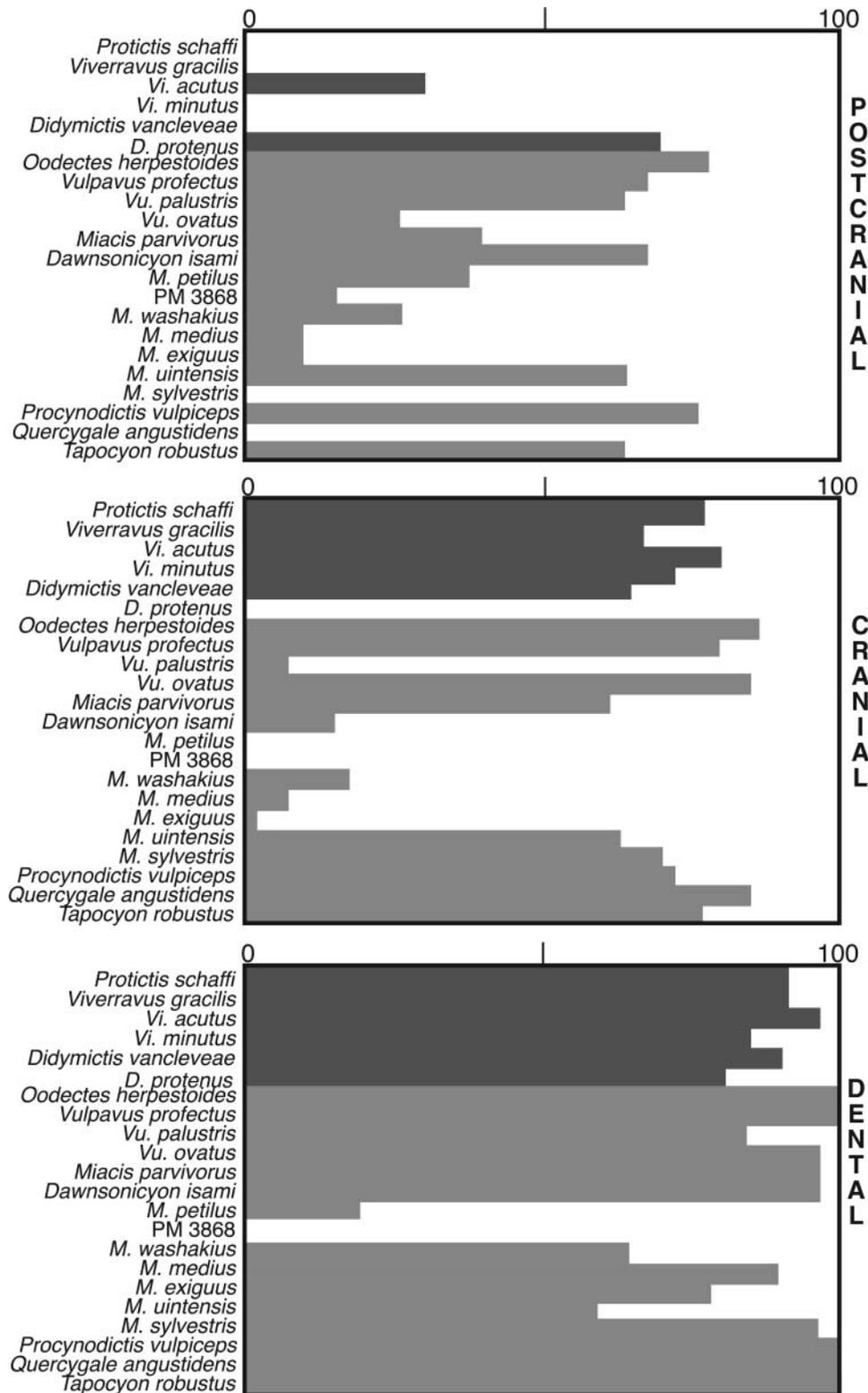
**Figure 3.** Character partitions – topologies derived from craniodental versus postcranial data: **A**, craniodental characters only (postcranial characters omitted); strict consensus of 904 trees of 463 steps each; **B**, postcranial characters only (craniodental characters omitted); strict consensus of 173 trees of 516 steps characters each.

strengthen support for previously identified hypotheses of relationships (for synapomorphies of this and other clades, see Table 1). Similarly, the addition of postcranial characters resolves previously ambiguous relationships, even though some taxa have substantial amounts of missing data.

The Carnivoraformes clade likewise is supported by both craniodental and postcranial synapomorphies. When taxa shared between the two analyses are compared, the most significant difference is a novel hypothesis of monophyly near the base of the carnivoraformes. A clade comprised of seven taxa (five of which were included in the craniodental study) is recovered. In the previous study these five taxa common to both analyses occurred as a para-

phyletic series of stem carnivoraformes. The newly identified clade ("Miacis" *petilus*, *Dawsonicyon*, *Miacis parvivorus*, *Oödetes herpestoides* and the three species of *Vulpavus*) is supported by two synapomorphies, both postcranial, emphasizing that craniodental features alone are insufficient to reconstruct relationships of these taxa. Within this clade, however, subclades are supported by data from both of the individual character subsets (postcranial versus craniodental). One character from each subset unites the subclade of the remaining five taxa at node 3, while *Oödetes* is united with the three *Vulpavus* species by one postcranial and three craniodental synapomorphies.

Certain craniodental characters that serve as synapomorphies in the present analysis were found to be homoplasious



**Figure 4.** Amount of known material of included basal carnivoramorph taxa for each character subset. Dark grey represents Viverravidae and light grey represents basal Carnivoraformes. While the Viverravidae are clearly represented by a higher percentage of craniodental information than postcranial, this is not true of the Carnivoraformes. The amount of known postcranial morphology is roughly equal to that of the crania for characters included in the matrix, with both represented far more than known dentition.



**Table 1.** Characters diagnosing nodes in the present analysis; only unambiguous synapomorphies listed. \* - Shared with Wesley-Hunt and Flynn (2005) diagnostic character listing for this node**Carnivoramorpha** (15 unambiguous synapomorphies; 7 postcranial, 1 cranial, 7 dental):

- Humerus – lesser tuberosity associated with a ridge of bone [115(0)]
- Humerus – reduced bicipital groove [122(1)]
- Ulna – flat radial notch [129(0)]
- Ulna – lack of a deep tendon groove on the proximal surface [131(1)]
- Carpus – proximal surface of scaphoid/scapholunar convex [145(0)]
- Pes – astragalar foramen present and dorsally located [182(0)]
- Pes – astragalar/tibial articular surface does not fully cover dorsal astragalus [185(1)]
- Cranial – palatine canal primary anterior opening at maxilla-palatine suture [6(1)]
- M1 – parastyle projects farther labially than metastyle [44(1)]
- M1 – parastylar shelf broad [51(1)]\*
- P4/m1 – carnassial shear present [54(1)]\*
- P4 – metastylar blade elongated [57(1)]
- P4 – protocone anterior to paracone [82(1)]\*
- Lower molars – m1 much larger than posterior dentition [86(1)]\*

**Viverravidae** (7 unambiguous synapomorphies; 3 postcranial, 1 cranial, 3 dental):

- Femur – lesser trochanter at the same level as the 3rd trochanter [158(1)]
- Femur – 3rd trochanter a clearly defined, robust feature [159(0)]
- Pelvis – ischial spine located near the border of the acetabulum [201(0)]
- Cranial – fossa for the stapedius muscle open and not well defined [37(1)]
- M1 – protocone equal or subequal to paracone height [42 (1)]\*
- P4 – parastylar cups well developed and defined [55(1)]\*
- m3 – lost [88(1)]\*

**Node V1** (1 unambiguous synapomorphy [cranial]):

- Cranial – postglenoid foramen located near edge of skull [11(1)]

**Carnivoraformes** (7 unambiguous synapomorphies; 5 postcranial, 2 dental):

- Humerus – lateral extension of capitulum on anterior not clearly distinguished [106(1)]
- Humerus – olecranon fossa deep and slot-like [107(1)]
- Humerus – medial edge of posterior trochlea vertical [108(0)]
- Humerus – delto-pectoral crest a clearly defined and high feature [109(0)]
- Humerus – capitulum not highly rounded in shape [123(0)]
- M1 – complete cingulum present around the lingual face of protocone [41(1)]
- m2 – talonid not elongated, no enlarged hypoconulid [59(1)]

**Node 1** (2 unambiguous synapomorphies [postcranial])

- Humerus – olecranon fossa shallow and circular [107(0)]
- Humerus – trochlea even with capitulum in distal expansion [116(0)]

**Node 2** (2 unambiguous synapomorphies [postcranial])

- Ulna - m. brachialis insertion site on anterior of shaft [128(0)]
- Ulna – distal anteromedial protuberance well developed [135(0)]

**Node 3** (2 unambiguous synapomorphies; 1 postcranial, 1 dental)

- Humerus – medial epicondylar curvature present [111(1)]
- P3 – no posterior accessory cusps present [58(2)]

**Node 4** (4 unambiguous synapomorphies; 1 postcranial, 3 dental)

- Humerus – capitulum rounded [123(1)]
- M1 – parastyle does not project farther labially than the metastyle [44(0)]
- P4 – protocone large and well developed [56(0)]
- P4 – metastylar blade short [57(0)]

**Node 5** (4 unambiguous synapomorphies; 1 postcranial, 3 cranial)

- Femur – proximal edges of condyles not flush with shaft [162(0)]
- Cranial – hypoglossal foramen anterior to groove anterior to occipital condyle [16(1)]
- Cranial – foramen ovale and alisphenoid canal separated by a thin wall [19(1)]
- Cranial – loop of internal carotid artery results in excavation in basisphenoid [23(1)]

**Node 6** (4 unambiguous synapomorphies; 3 postcranial, 1 dental):

- Ulna – radial notch curved [129(1)]
- Ulna – distal flanges on shaft reduced or absent [130(1)]
- Pes – fibular facet of astragalus crescent shaped [175(1)]
- M1 – parastyle projects buccally [45(1)]

*(Continued on next page)*

**Table 1.** Characters diagnosing nodes in the present analysis; only unambiguous synapomorphies listed. \* - Shared with Wesley-Hunt and Flynn (2005) diagnostic character listing for this node (*Continued*)

## Node 7 (1 unambiguous synapomorphy [cranial]):

Cranial – fossa present for anterior crus of ectotympanic [32(1)]

## Node 8 (6 unambiguous synapomorphies; 4 postcranial, 1 cranial, 1 dental):

Humerus – greater tuberosity extends past the humeral head [112(0)]  
 Humerus – supinator crest present and large [114(0)]  
 Phalanges – medial phalanx distal articulation surface asymmetrical [153(1)]  
 Femur – patellar groove shallow and not bound by ridges [166(0)]  
 Cranial – apron shelf on promontorium present and blunt [26(1)]  
 M2 – reduced to half the size of M1 or less [52(1)]

## Node 9 (4 unambiguous synapomorphies; 2 cranial, 2 dental):

Cranial – palatine canal anterior opening through maxilla [6(2)]  
 Cranial – foramen ovale and alisphenoid canal far apart [19(0)]  
 M3 – absent [53(1)]  
 m3 – absent [88(1)]

## Carnivora + Nimravidae (7 unambiguous synapomorphies; 6 postcranial, 1 dental):

Cranial – parietal equal or subequal in length to frontal at midline [7(1)]  
 Cranial – fenestra cochleae posterior to mastoid tubercle [18(0)]  
 Cranial – promontorium anteriorly blunt [28(2)]  
 Cranial – fossa present for anterior crus of ectotympanic [32(1)]  
 Cranial – flange on basioccipital lateral edge well developed [34(2)]  
 M1 – lacking a defined cingulum around the lingual face of the protocone [41(0)]  
 Cranial – expanded braincase, fronto-parietal suture more anteriorly located [66(1)]

## Carnivora (9 unambiguous synapomorphies; 7 postcranial, 2 cranial):

Humerus – delto-pectoral crest reduced [109(1)]  
 Ulna – deep tendon groove on proximal end of shaft present [131(0)]  
 Tibia – inner condylar borders do not contact one another [171(1)]  
 Pes – astragalus articular surface with tibia covers entire dorsal surface [185(0)]  
 Pes – calcaneus with a well-developed peroneal tubercle [189(0)]  
 Pes – calcaneus posterior facet with two distinct angles [194(1)]  
 Pelvis – anterior lateral ilium lacks a dividing ridge [204(1)]  
 Cranial – posterior palatine extends past the upper tooth row [5(0)]  
 Cranial – bone between the mastoid process and paroccipital process laterally wide with a rugose surface [33(1)]

## Caniformia (12 unambiguous synapomorphies; 7 postcranial, 4 cranial, 1 dental):

Humerus – ulnar collateral ligament insertion site very large [120(0)]  
 Carpus – metacarpal III fails to overlap IV proximally [148(0)]  
 Phalanges – medial phalanx with a symmetrical distal articulation surface [153(0)]  
 Phalanges – lack excavation of the medial phalanx on the lateral margin [155(0)]  
 Pes – astragalus lateral margin lacks an anterior ventral expansion [179(1)]  
 Pes – cuboid articulation with metatarsal V at least 40% of the distal surface [195(1)]  
 Cranial – palatine canal opens through maxilla-palatine suture [6(1)]  
 Cranial – posterior lacerate foramen a defined foramen, not a vacuity [17(1)]  
 Cranial – promontorium anteriorly elongate with a broad flat extension [28(3)]  
 M1 – posterior lingual cingular shelf larger than anterior segment [47(1)]  
 Cranial – maxilloturbinals large and branching [62(1)]\*  
 Baculum – long and stylized [89(1)]

## Feliformia (13 unambiguous synapomorphies; 5 postcranial, 5 cranial, 1 dental, 2 soft anatomy):

Radius – capitular eminence is very minor [142(0)]  
 Carpus – unciform equal in width to magnum [146(1)]  
 Carpus – cuneiform articulates with ulna on radial margin [150(0)]  
 Femur – lesser trochanter reduced in size [163(1)]  
 Vertebrae – atlas transverse processes extend posteriorly at a sharp angle [208(1)]  
 Cranial – lacrimal facial process is not present on the face [1(2)]  
 Cranial – paroccipital process laterally flattened [10(1)]  
 Cranial – anterior loop of internal carotid artery absent [23(0)]  
 Cranial – ventral process of promontorium present and medially positioned [27(1)]  
 M1 – protocone equal or subequal in size to paracone [42(1)]  
 Cranial – carotid artery enters auditory bulla anteriorly, without an enclosing tube [67(3)]  
 Soft anatomy – Cowper's gland present [95(1)]  
 Soft anatomy – prostate gland large, with ampulla, and bilobed [96(1)]

in the previous craniodental-only analyses (Wesley-Hunt & Flynn 2005; Spaulding *et al.* 2010). Here the addition of postcranial characters served to reveal ‘hidden support’ (see Gatesy *et al.* 1999, 2003) in the craniodental partition. The different resultant topologies do not indicate that the two datasets conflict substantially with one another; quite the opposite, as this newly found monophyletic clade did have hidden support in the pre-existing character partition.

In addition to newly identifying a basal monophyletic clade of seven carnivoraform taxa (node 1), the incorporation of postcranial characters yields much greater resolution, in both the stem carnivoramorphans and crown taxa, than did the craniodental based analysis of Spaulding *et al.* (2010). The more crownward topology recovered compares favourably with that of the Wesley-Hunt & Flynn (2005) study. The lack of resolution found in later papers utilizing this matrix (such as Spaulding *et al.* 2010) is most likely due to the incorporation of two taxa represented by a relatively high amount of missing data (low proportion of craniodental material present in these taxa). This demonstrates that postcranial characters are essential for better resolving relationships at both higher and lower hierarchical levels if taxon sampling is expanded beyond all but the most completely preserved fossils.

In this analysis the Nimravidae are the nearest outgroup to Carnivora. Previously the Nimravidae has been assigned to a variety of positions, none with robust support, including as members of the Caniformia (Flynn & Galiano 1982), basal Feliformia (Wesley-Hunt & Flynn 2005), and in its present position outside the crown Carnivora (see also Neff 1983; Bryant 1991). Previous analyses using only the craniodental source matrix found the Nimravidae to be either a member of the Feliformia (Wesley-Hunt & Flynn 2005) or *incertae sedis* within Carnivora (Wesley-Hunt & Werdelin 2005; Spaulding *et al.* 2010). Placement of this group outside of the Carnivora is strongly supported in the present analysis. Nine characters (seven postcranial and two craniodental) serve as synapomorphies of Carnivora to the exclusion of the nimravids.

Comparing the topology within the crown group between the two studies, we find no change within the Feliformia, but marked changes within the Caniformia. As in other parts of the carnivoramorph phylogeny, where previously there was a lack of resolution within this clade, the current analysis yields a completely resolved topology. The sole species of amphicyonid sampled groups with the canids, whereas in the craniodental analysis of Wesley-Hunt & Flynn (2005) it was the first diverging lineage within the Caniformia. Within Arctoidea markedly different topologies occur between analyses based on the two datasets, including differences beyond simply resolving polytomies. Instead of being the nearest outgroup to Musteloidea, the pinnipeds resolve several nodes deeper within Arctoidea, as nearest outgroup to a clade of Ursidae (*Ursus*) plus Ailuridae (*Ailurus*), and relationships among mustelids and

their relatives differ substantially. When the morphologically based interrelationships of this study are compared with that of recent molecular work (Flynn *et al.* 2005), the unrooted network topology within arctoids shows a higher degree of congruence. This is not the case with the previous craniodental based analysis (Spaulding *et al.* 2010).

While topological differences between the two datasets could be considered to be due to the more ‘functional’ nature of the postcranial characters, such a presumption has little empirical or conceptual support, as the dentition and cranium obviously must have functional aspects as well (for an empirical analysis testing similar arguments for dental versus basicranial characters, see Wesley-Hunt & Flynn 2005). The majority of nodal support values in this study show congruence between the two character subsets in their contributions to the nodal support. For example, both postcranial and dental features support linkage of the relatively arboreal *Vulpavus* (Heinrich & Rose 1997) with other taxa having similar inferred locomotor styles, such as *Oödetes*. It is noteworthy that this clade shares both postcranial features reflecting an arboreal locomotor style and dental features reflecting a reduction in the sectorial capacity of the dentition (presumably related to omnivory), suggesting that both phylogenetic heritage and ecological specializations are reflected accurately in the anatomy of this clade. This congruence of support across different character partitions holds for many other nodes in the analyses, each of which has substantial support from all three character partitions evaluated in this study (Table 1). There are only two nodes in the phylogeny that are supported only by postcranial characters, all of which are within the non-carnivoran carnivoraforms (nodes 1 and 2) which contain PM 3868 either at the base or as an immediate outgroup, and thus it is impossible for craniodental characters to optimize at this node, as PM 3868 is represented by only postcranial morphology. There are four nodes with only cranial or dental support: one within Viverravidae (node V1), two within basal Carnivoraformes (nodes 7 and 9) and the node grouping the nimravids with Carnivora. All clades at these nodes likewise contain taxa with no postcranial data as the first branch within the clade or as the immediate outgroup taxon. Due to this distribution of known morphology, as with the previous nodes (1 and 2), it would be impossible for postcranial information to optimize unambiguously at these nodes. Acctran or Deltran optimizations would optimize characters from the ‘missing’ character system, but here we are presenting only unambiguous synapomorphies.

The high level of agreement in nodal support among characters from different partitions highlights the importance of sampling morphological characters from all parts of organisms, and shows that even though distinct topologies may be supported by characters from different partitions, a total evidence approach often reveals the ‘hidden support’ for other topologies retained within each character partition. In addition, a total evidence analysis is methodologically and

philosophically preferable, as there is no reason to artificially segment available data in the building of phylogenetic trees (see discussion in Gatesy *et al.* 1998, 2003; O'Leary 1999).

We detail all novel character optimizations and distributions from the analyses in this study in the Appendix, but here we discuss in more detail a few characters that have played a prominent role in prior locomotor or functional analyses. One such system includes fully retractile claws, as occur in some modern feliforms. Wesley & Flynn (2003) provided compelling evidence for the presence of retractile pedal claws in the early fossil carnivoraform *Taypocyon*, based on the presence of an asymmetrical articular surface of the distal medial phalanx and an embayment in its lateral shaft (characters 54 and 56, respectively, in this analysis). Character 54 unites the clade at node 8: *Tapocyon*, *Quercygale*, nimravids and Carnivora, with a reversal characterizing the Caniformia clade within Carnivora. The derived state of character 56, presence of an embayment of the lateral shaft of the distal medial phalanx, has an uncertain reconstruction at the Carnivoraformes node; while the derived state does not occur in any taxon outside this clade, medial phalanges are not preserved for any basal-most member (in the shortest trees) of this clade. As such, it is uncertain if the derived state is primitive for Carnivoraformes or if it was independently derived in *Dawsonicyon* and the clade at node 5, including *Miacis uintensis* plus Carnivora, as *Vulpavus* does not have this embayment. As in character 54, a reversal to the primitive condition of this feature unites the Caniformia. These results not only support the hypothesis of Wesley & Flynn (2003) that retractile claws were primitive for the Carnivora, but the more comprehensive taxon and character sampling of this study allows us to reconstruct the steps by which this transformation was accomplished: first the shaft of the medial phalanx became asymmetrical (embayed), then the distal articular surface of the bone attained asymmetry.

## Conclusions

This study demonstrates the general importance of more comprehensive character sampling, and in particular the value of adding postcranial characters (previously almost ignored in higher-level phylogeny analyses for this clade), for better resolving and providing stronger nodal support for the phylogeny of the Carnivoramorpha. The addition of postcranial characters also permits incorporation of a number of taxa that previously could not be analysed, and numerous prior studies have documented the importance of also increasing taxon sampling (even taxa with incomplete character representation) to more accurately reconstruct phylogeny (i.e. Kirsch & Archer 1982; Gauthier *et al.* 1988). One especially noteworthy result is the resolution of,

and strong support for, the position of problematic clades such as the Nimravidae.

All analyses performed with the combined matrix recover the Carnivoraformes, offering substantial corroboration for this recently named and phylogenetically defined clade (in Flynn *et al.* 2010). The addition of postcranial characters to prior matrices heavily dominated by craniodental characters resulted in generally enhanced resolution when compared with phylogenies based only on craniodental data (as in Spaulding *et al.* 2010). For example, resolution of interrelationships within the Viverravidae was substantially increased, and enhanced character sampling recaptures resolution that had been lost in previous studies of basal Carnivoraformes that only increased taxon sampling without adding new, potentially phylogenetically informative characters.

By adding numerous postcranial characters, we now have incorporated and resolved the relationships of many basal Carnivoraformes taxa that previously could not have been included in phylogenetic analyses based almost exclusively on craniodental characters (Fig. 3). For example, we have identified a monophyletic subset of basal Carnivoraformes, a clade not found in previous analyses; this novel grouping yields a revised reconstruction of character polarity at the base of Carnivoraformes and Carnivoramorpha. In addition, the position of Nimravidae as a late-diverging member of the Carnivoraformes clade, but not a member of crown Carnivora, receives substantial support, resolving long-standing ambiguity in the phylogenetic position of this enigmatic group of sabre-toothed carnivoramorphans.

We have identified many novel postcranial synapomorphies of the Carnivoramorpha and subclades within this group. With these advances, and by expanding taxonomic sampling and seeking additional phylogenetically informative characters, we may soon arrive at a time when isolated postcranial remains, such as a single long bone, can be confidently assigned to a taxonomic group with Carnivoramorpha, similar to the situation beginning to be achieved in archosaurs (e.g. Irmis *et al.* 2007). The fossil record of the early Eocene and Palaeocene is rich with isolated material, and the ability to recognize the phylogenetic affinity of such specimens, even if only at a relatively coarse scale, would allow us to greatly improve faunal lists of fossil localities, enhance taxonomic diversity studies, and more accurately identify the first and last known occurrences of taxa and their geographic ranges.

This analysis also clearly highlights parts of the phylogeny of Carnivoramorpha that still require additional data to better resolve interrelationships or provide enhanced support for already recognized clades. One such area is the basal carnivoraforms. While we have clearly demonstrated that incomplete taxa can be beneficial to a phylogenetic analysis of the early diverging carnivoramorphans, there is still a large polytomy at the base of this clade in the strict consensus tree. Our expanded morphological

data matrix for Carnivoramorpha, adding substantial numbers of postcranial characters to complement the recent substantial suite of cranial characters provided by Wesley-Hunt & Flynn (2005), has created an unusual situation in mammalian ordinal-level systematics – one in which the dental subset is now the most poorly represented suite of characters. Future work on the Carnivoramorpha will have to expand the matrix to include many dental characters previously utilized as diagnostic features or synapomorphies at lower taxonomic levels, particularly for Viverravidae and basal Carnivoraformes.

Nonetheless, the present study represents the most expansive character analysis of this group to date. The resultant phylogeny, and future analyses made possible by this expanded morphological character set, will be important in reconstructing a variety of evolutionary transformations, such as the evolution of brain and body size, locomotor mode, life histories, biogeography, etc. This dataset already has proven especially useful in studies of locomotion in basal carnivoramorphans. Because we have included postcranial characters in the analysis itself, we now can ascertain if morphological features hypothesized to indicate locomotor styles are primitive or derived in an individual taxon. Thus, it is possible to reconstruct locomotor styles within a phylogenetic context. This will allow us to hypothesize if a locomotor mode, such as arboreality, was acquired in the same or different ways during multiple convergent acquisitions. Similarly, we can assess whether features that co-vary with locomotor styles in living taxa always do so in fossils, or if they occur in different combinations reflecting both locomotor habitus and inheritance from ancestral conditions which may reflect different locomotor styles.

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## Appendix

Characters and states, with descriptions and distributional information. Source for character, either a prior phylogenetic analysis or new to this study in parentheses following character name. Exemplar taxa for each state indicated in parentheses following state description; complete distributions in study taxa indicated in matrix (matrix available online at [www.morphobank.org project 367](http://www.morphobank.org/project/367)).

Characters 1–99 in the current study correspond to characters 1–99 in Wesley-Hunt & Flynn (2005). Refer to that study for details of those additional characters.

100: Scapula – supraglenoid tubercle morphology (Heinrich & Rose 1997): 0 – expands out over the glenoid fossa (*Didymictis*); 1 – blunt, does not extend over the glenoid fossa (*Vulpavus*)

An expansion of the supraglenoid tubercle is plesiomorphic for Carnivoramorpha. Its reduction unites the species of *Vulpavus* with *Oödectes*, and is seen convergently in *Miacis uintensis*, *Nandinia*, *Hesperocyon*, and unites most arctoids, with the exceptions of *Gulo* and *Ailurus*.

101: Scapula – acromion process angle (new): Either or a short or a long process can be dorsally directed at the acromion process apex, or remain in the same plane as the scapular spine: 0 – process angles dorsally (*Vulpavus*); 1 – process remains in same plane as the scapular spine (*Canis*)

A process that does not angle dorsally appears to be primitive for Carnivoramorpha, but this feature generally is not preserved in fossils. A basal carnivoraform clade has this morphology (node 1), based upon *Oödectes* and *Dawsonicyon*. A dorsally directed process also unites the nimravids, and appears independently in *Daphoenus* and *Ailurus*.

102: Scapula – acromion process length (Wang 1993): The acromion process can terminate far distally to the glenoid fossa or terminate at or before the border. A long acromion can be used as a proxy for the presence of clavicles in extinct taxa. 0 – process extends past glenoid fossa (*Vulpavus*); 1 – process terminates before or at glenoid fossa (*Gulo*)

Information for the polarity of this character at the base of Ferae is lacking, although the non-Ferae outgroups possess a shorter process. All non-crown Carnivoraformes for which this feature can be observed have a long acromion, with the exception of *Procynodictis*. The process evolved to a shortened state at the node uniting the nimravids with Carnivora, with longer processes reappearing in *Daphoenus* within Carnivora.

103: Scapula – coracoid process (Heinrich & Rose 1997): 0 – present, as a large clearly projecting process (*Felis*); 1 – extremely small or absent (*Canis*)

A large process is plesiomorphic for Carnivoramorpha. Feliforms and *Canis* both have a smaller process, with arctoids showing larger structures. However, it is unclear if the arctoid condition is a reversal or if the reduced structure in both feliforms and *Canis* is a convergence. Within Feliformia there is a reversal to a large structure in *Felis*.

104: Scapula – scapular spine morphology (new): Coded while viewing the spine from a ventral view of the scapula. 0 – spine forms one continuous, smooth, downward curve (*Oödectes*); 1 – spine has a dip or embayment in the curve (*Herpestes*); 2 – spine has a sharply angled drop rather than a smooth downward slope (*Mephitis*)

While this character currently is not phylogenetically informative in the present taxon sampling focused on early carnivoraformes, state 1 occurs in many herpestids and state 2 is characteristic of mephitids.

105: Scapula – metacromion process (new): 0 – present and well developed (*Herpestes*); 1 – weak or absent (Otariidae)

A well-developed metacromion process is primitive for Carnivoramorpha. Its reduction unites the pinnipeds, and is seen independently in *Ursus*, *Canis*, *Hyaena* and *Civettictis*.

106: Humerus – indentation on the anterior surface of the capitulum (new): 0 – present (*Hyaenodon*); 1 – absent (*Vulpavus*)

This feature, marked by a clear proximal projection of the capitulum and best seen in anterior view, indicates the lateral extension of the capitulum. When the humerus is viewed anteriorly, a depression is clearly seen on the dorsal margin of the capitulum. The presence of this indentation is primitive for Ferae. At the Carnivoraformes node the feature is lost, and remains so, with the exception of three isolated reversals seen in *Hoplophoneus*, *Canis* and *Ursus*.

107: Humerus – olecranon fossa shape (Matthew 1909): 0 – shallow and round (*Vulpavus*); 1: deep and slot-like (*Miacis uintensis*); 2 – perforated (*Didymictis*)

A perforated olecranon fossa is primitive for Carnivoramorpha. The perforation is lost in carnivoraformes, with a ‘shallow and round’ morphology attained in the clade containing *M. petilus* and *Vulpavus* (node 2). Canids regain a perforated fossa, as do the following taxa independently: *Procyon*, *Ailurus*, and feliforms at the node containing *Civettictis* and *Hyaena* (with the exception of *Felis*).

108: Humerus – medial edge of posterior trochlea (new): 0 – vertical (*Vulpavus*); 1 – slanted (*Oödectes*)

A slanted boundary is plesiomorphic for Carnivoramorpha. A vertical boundary unites the species of *Vulpavus*, with isolated appearances in other basal carnivoraformes. A vertical boundary is plesiomorphic for the crown and there

is a reversal to a curved morphology within some arctoids and *Felis*.

109: Humerus – delto-pectoral crest (Matthew 1909): 0 – present (*Vulpavus*); 1 – absent (*Didymictis*)

Lack of a crest is primitive within Carnivoraformes, as all basal carnivoraforms with the exception of *Procyonodictis* possess this feature, with a reversal uniting the crown Carnivora. A crest is again present in *Daphoenus* and pinnipeds.

110: Humerus – medial epicondyle (Matthew 1909): 0 – ends with a well rounded head (*Vulpavus*); 1 – poorly defined, appearing more like a blunt tubercle (*Didymictis*)

The presence or absence of this feature is best defined by considering the medial border. When the feature is well developed it projects distinctly; when it is not, there is no medial expansion and the medial border of the epicondyle ‘flows’ uninterrupted into the medial border of the bone. Primitively for the taxa sampled the medial epicondyle has a well-rounded head. A reduction is seen independently in *Didymictis* and *Procyonodictis* outside of the crown Carnivora. The primitive state for Carnivora is ambiguous, as many feliforms and most caniforms have a reduced medial epicondyle.

111: Humerus – medial epicondyle orientation (new): 0 – lacks curvature (is straight) (*Oödectes*); 1 – curves anteriorly (*Vulpavus*); 2 – curves posteriorly (*Didymictis*)

The majority of carnivoramorph taxa have an epicondyle that curves posteriorly, a subset of basal carnivoraforms instead lack curvature, with the species of *Vulpavus* being united by an anterior curvature. *Nandinia* also lacks curvature.

112: Humerus – greater tuberosity height (Heinrich & Rose 1997): 0 – extends past head (*Didymictis*); 1 – flush with head in height (*Vulpavus*)

A high greater tuberosity is primitive for the Carnivoramorpha; there is a reduction at the Carnivoraformes node. A reversal to a high tuberosity occurs at the *Tapocyon* + Carnivora node (node 8). Within the Carnivora, a low tuberosity unites most arctoids.

113: Humerus – posterior trochlea (new): 0 – not bound by high ridges (*Oödectes*); 1 – bound by high ridges (*Canis*)

Primitively in Carnivoramorpha, the posterodistal articular surface of the humerus is not bound medially or laterally by high ridges. Possession of high ridges unites *Otarocyon* and *Canis*, most arctoids, and is found independently three times within Feliformia.

114: Humerus – brachial flange (Heinrich & Rose 1997): 0 – present and large, extending out from the body of the

bone as a flat surface (*Vulpavus*); 1 – small, nothing but a small raised line of bone (*Didymictis*)

The lack of this feature is primitive for Carnivoramorpha. A large flange groups a subset of basal carnivoraforms and unites the Carnivora with the nimravids and *Tapocyon* (node 8). A reversal to a small flange is seen in scattered crown carnivoran taxa.

115: Humerus – lesser tuberosity with a crest or ridge of bone leading from this feature down the shaft (new): 0 – present (*Didymictis*); 1 – absent (*Canis*)

A lack of the ridge is primitive for outgroup taxa, and the feature first occurs at the base of Carnivoramorpha. The nimravids are united by loss of the ridge, and while polarity of this character is ambiguous for crown Carnivora, the arctoids are united by the loss (with an apparent regain in pinnipeds).

116: Humerus – trochlea extent (Heinrich & Rose 1997): 0 – extends distally past capitulum when viewed anteriorly (*Didymictis*); 1 – two articular surfaces are more inline (*Vulpavus*)

A larger trochlea than capitulum is primitive for Carnivoramorpha. A subset of basal carnivoraforms is united by the reduction of the trochlea, and this feature is seen in isolated crown Carnivora taxa as well.

117: Humerus – epicondylar foramen (new): 0 – absent (*Canis*); 1 – present and round (*Hyaenodon*); 2 – present and elongated (*Vulpavus*)

Presence of a foramen is primitive for Ferae. Both creodonts included in this study have a round foramen, while all carnivoramorphans with the foramen have the elongated condition. The foramen is lost in some caniforms.

118: Humerus – distal L-shaped ridge of bone on capitulum in distal view (new): 0 – present (*Vulpavus*) 1 – absent (*Felis*)

The presence of this ridge is plesiomorphic for Carnivoramorpha. It is lost in *Canis*, many arctoids, and the feliform clade compromised of *Hyaena*, *Felis* and *Herpestes*.

119: Humerus – orientation of bone on the lateral distal margin (new): 0 – faces laterally (*Hyaenodon*); 1 – faces posteriorly (*Vulpavus*)

In Ferae as a whole the bone appears to face laterally, although the optimization for Carnivoramorpha is ambiguous. *Didymictis* has a laterally facing surface, and basal carnivoraforms with the exception of *Procyonodictis*, have a posteriorly facing surface. All crown Carnivora studied, with the exception of *Mephitis* and *Ursus* likewise have a posteriorly facing surface.

120: Humerus – ulnar collateral ligament insertion site size (Heinrich & Rose 1997); 0 – very large, forming a distinct

circular pit (*Didymictis*); 1 – small, forming only a shallow depression (*Vulpavus*)

The primitive state of this character is ambiguous. However for the Carnivora, a small depression is primitive, with a large pit characterizing caniforms.

121: Humerus – greater tuberosity angle (Heinrich & Rose 1997): 0 – greater tuberosity angled away from head; smooth arch is not formed with lesser tuberosity (*Didymictis*); 1 – greater tuberosity more flush with head (*Vulpavus*)

An angled greater tuberosity is primitive for the study sample. Among the Viverravidae no agreement is reached, as *Viverravus* exhibits the opposite state from *Didymictis*. A greater tuberosity flush with the head groups a subset of basal carnivoraforms.

122: Humerus – prominence of bicipital groove (Taylor 1974): 0 – groove is very noticeable and deep (*Nandinia*); 1 – groove is very subtle if noticeable at all (*Civettictis*)

A deep groove is primitive for Ferae, and a subtle one develops early in the history of Carnivoramorpha. A subtle groove reappears in arctoids, with the exception of *Gulo* and pinnipeds. Of the feliforms, both *Nandinia* and *Herpestes* have a deep groove.

123: Humerus – capitulum shape (Heinrich & Rose 1995): 0 – flat for the whole length with a uniform distal margin (*Thinocyon*); 1 – rounded (*Vulpavus*)

A rounded capitulum is primitive for Ferae and Carnivoramorpha, with a flat shape ancestral for Carnivoraformes. Within carnivoraforms a reversal to the round condition groups *Oödictes* and the species of *Vulpavus* (node 4). A rounded capitulum also reappears in the feliforms to the exclusion of *Nandinia*.

124: Humerus - tricipital line (new): 0 – large and distinctive (*Didymictis*); 1 – reduced (*Nandinia*)

A distinctive tricipital line is primitive for carnivoramorphans, with a reduction supporting the grouping of a subset of basal carnivoraforms. The majority of the rest of the study taxa have a distinct line, with the exception of *Hoplophoenus*, *Procyon* and *Nandinia*.

125: Ulna – semi-lunar notch distal border morphology (new): 0 – W-shaped distal border; an indentation occurs between the articular surface with the radius and the rest of the facet (*Oödictes*); 1 – indentation lacking (*Canis*)

The presence of the indentation is primitive for Ferae, and ambiguous in its optimization for Viverravidae. Within Carnivoraformes, the lack of a notch unites canids and *Daphoenus*, and appears in a few unrelated additional taxa.

126: Ulna – semi-lunar notch proximal border extent (new): 0 – proximal ridge extends far from shaft surface

(*Hyaenodon*); 1 – proximal ridge flush with shaft surface (*Oödictes*)

The primitive state of this condition is ambiguous. A ridge extending far from the shaft surface is found in creodonts sampled in this study, and a reduced ridge is primitive for carnivoramorphans. The creodont-like state occurs in several feliforms, and *Ursus* together with *Ailurus* within caniforms.

127: Ulna – m. brachialis insertion site (new): 0 – present (*Vulpavus*); 1 – absent (*Ailurus*)

The presence of a slit on the ulna, hypothesized to be for the insertion of the m. brachialis muscle, is primitive. Feliforms lack this feature, with the exception of *Civettictis*, and it also is present in many arctoids.

128: Ulna – m. brachialis insertion site position (new): 0 – on anterior surface of ulna (*Vulpavus*); 1 – on the lateral margin of the shaft (*Oödictes*)

The primitive condition for Carnivoramorpha and Carnivoraformes is an insertion site on the lateral side of the shaft. A subset of basal Carnivoraformes, Nimravids and arctoids separately develop an insertion on the anterior surface of the bone.

129: Ulna – radial notch curvature (Heinrich & Rose 1997): 0 – absent (*Vulpavus*); 1 – present (*Ailurus*)

A flat radial notch is primitive for Carnivoramorpha, although a curved one is found in outgroup taxa, including the creodonts. Within the study clade, the node containing *Procynodictis* and the Carnivora (node 6) is marked by the acquisition of a curved surface on the ulna for the radial head.

130: Ulna – flange presence on distal region of the shaft (Matthew 1909): 0 – two flanges present and well defined (*Vulpavus*); 1 – flanges absent (*Ailurus*)

Large flanges are primitive for Carnivoramorpha. *Procynodictis* has no flanges, shared by many taxa past this specimen on the cladogram. Within the Carnivora, reacquisition of flanges occur independently in two the extinct canids and *Nandinia*. No taxa in this study possess only a single flange.

131: Ulna – deep tendon groove on proximal end of ulna (Heinrich & Rose 1997); 0 – present (*Hyaenodon*); 1 – absent (*Vulpavus*)

The lack of a deep groove unites Carnivoramorpha, with outgroup taxa having a deep groove. *Procynodictis* and Carnivora separately reacquired the deep morphology, with a return to the shallow condition seen in some Arctoidea.

132: Ulna – olecranon process shape (new): 0 – mediolaterally robust, square in shape (*Vulpavus*); 1 – mediolaterally compressed (*Felis*)

A compressed olecranon process is primitive for Carnivoramorpha, while the robust and square state unites a subgroup of basal carnivoraforms. The robust condition also occurs independently in *Tapocyon*, *Mephitis*, *Procyon* and *Gulo*.

133: Ulna – anconeal process extent (Heinrich & Rose 1997): 0 – projecting from the shaft, shelf like (*Didymictis*); 1 – flush with shaft (*Vulpavus*)

Primitively, the anconeal process is shelf-like. An apparent reduction of this process characterizes a subgroup of basal carnivoraforms. The reduction was independently attained in *Canis*, and *Ursus* plus *Ailurus*.

134: Ulna – proximal border of semi-lunar notch, position (new): 0 – lateral to the shaft (*Hyaenodon*); 1 – centred with respect to the shaft (*Oödictes*)

A shift to the lateral side of the bone is seen in creodonts. This morphology also appears in scattered taxa within the crown Carnivora.

135: Ulna – anteriomedial protuberance development (Taylor 1974): 0 – well developed (*Nandinia*); 1 – small (*Canis*)

A small process is primitive for Carnivoramorpha, with the separate acquisition of a well-developed protuberance in one monophyletic subclade of basal carnivoraforms and also unites *Tapocyon* with the crown carnivoraforms (node 8). Within Carnivora re-acquisition of a small process unites the arctoids (while *Ursus* has a well developed protuberance).

136: Ulna – groove on lateral side of shaft (new): 0 – present (*Hyaenodon*); 1 – absent (*Vulpavus*)

A groove on the lateral side of the shaft is found in creodonts and *Didymictis*. The lack of this groove serves as a synapomorphy for Carnivoraformes.

137: Ulna shape – sigmoidal (Matthew 1909); the ulna is used as a proxy for the curved nature of all forelimb bones noted by Matthew (1909): 0 – sigmoidal (*Vulpavus*); 1 – straight (*Canis*)

A highly curved, sigmoidal ulna is a synapomorphy of the *Vulpavus* clade. The only other taxon to exhibit this morphology is *Nandinia*.

138: Ulna – radial notch orientation (Heinrich & Rose 1997); 0 – faces anteriorly (*Didymictis*); 1 – faces more laterally (*Vulpavus*)

An anteriorly facing notch is plesiomorphic for Carnivoramorpha. The more laterally directed feature occurs in all basal carnivoraforms with the exception of *Miacis washakius*. Within the crown an anteriorly facing notch unites feliforms other than *Nandinia*, and occurs independently in various caniforms.

139: Radius – radial head shape (Heinrich & Rose 1997): 0 – round (*Vulpavus*); 1 – oval (*Didymictis*)

An oval head is primitive for Carnivoramorpha. A rounded head unites the species of *Vulpavus* with *Oödictes* (node 4). A round head is also seen in *Dawsonicyon*, *Miacis uintensis* and *Nandinia*.

140: Radius – distal articular surface shape (Heinrich & Rose 1997): 0 – round; if any elongation is present, it is oriented anteroposteriorly (*Didymictis*); 1 – elongated mediolaterally (*Vulpavus*)

Currently this character is phylogenetically uninformative, as the round condition is seen only in one species of *Didymictis*. However, it could prove to be a Viverravidae synapomorphy upon sampling other viverravid taxa.

141: Radius – large scaphoid articulation surface (Heinrich & Rose 1997): 0 – present (*Didymictis*); 1 – surface small (*Vulpavus*)

An expanded articulation surface for the scaphoid on the radius is found in the creodonts and *Didymictis*. Most basal Carnivoraformes have a reduced articular surface, though it is ambiguous if this is a synapomorphy of the group due to missing data. Nimravids and Carnivora share an expanded surface.

142: Radius – capitular eminence of radial head development (Heinrich & Rose 1997); 0 – small (*Vulpavus*); 1 – large, disrupts radial rim (*Canis*)

A large eminence is primitive for the taxa in this study; reduction to a smaller size serves as a synapomorphy for *Vulpavus*. A small eminence occurs independently in arctoids (with the exception of *Gulo* and *Ursus*), and in feliforms, with a reversal in *Herpestes*.

143: Radius – distal articulation surface shape (new) 0 – with a deep sulcus (*Erinaceus*); 1 – smooth, lacks a deep sulcus (*Vulpavus*)

A radius with a deep sulcus in the distal articulation surface is seen in outgroup erinaceamorphs.

144: Carpus – cuneiform shape in proximal view (Taylor 1974): 0 – triangular (*Nandinia*); 1 – rectangular (*Vulpavus*)

In the present analysis the derived triangular shape of the cuneiform is seen only in *Nandinia* and *Daphoenus*.

145: Carpus – proximal surface of scapholunar, curvature (Taylor 1974): 0 – fully convex (*Nandinia*); 1 – convex and concave (*Herpestes*)

A purely convex scapholunar proximal surface is primitive for Carnivoramorpha. A concave portion of the bone is primitive for non-*Nandinia* feliforms, but is fully convex in *Felis* (and *Nandinia*).

146: Carpus – uniciform width (new): 0 – as wide as trapezoid and magnum combined (*Canis*); 1 – small, only as wide as magnum alone (*Nandinia*)

A small uniciform is a synapomorphy of Feliformia. Primitively for Carnivoramorpha, the uniciform is much larger than surrounding carpals.

147: Carpus – trapezium position (Yalden 1970): 0 – on the posterior surface of the trapezoid (*Canis*); 1 – on the radial surface of the trapezoid (*Felis*)

As this character cannot be coded presently in any basal carnivoramorph taxa, the ancestral condition is unknown. Among the crown taxa, most arctoids possess a radial position of the trapezium.

148: Carpus – metacarpal III overlaps IV proximally (Bryant 1991): 0 – absent (*Canis*); 1 – present (*Vulpavus*)

In outgroup taxa this overlap is absent. There is a lack of data for the base of Carnivoramorpha, but in Carnivoraformes this overlap is present. It is absent again in Caniformia, with a separate loss in *Hyaena* among feliforms.

149: Carpus – distal surface of scapholunar shape (Yalden 1970): 0 – relatively smooth/even (*Canis*); 1 – a sharp projection exists between the magnum and trapezoid (*Ursus*)

Primitively the projection exists, and it is lost independently in some Caniformia (*Canis*, *Mephitis*, and *Ailurus*).

150: Carpus – cuneiform articulation with ulna, position (Yalden 1970): 0 – on medial (radial) margin (*Felis*); 1 – on distal surface of ulna (*Ursus*)

An articulation with the distal surface of the ulna is plesiomorphic for Carnivoramorpha, with feliforms (to the exclusion of *Herpestes*) united by a medial (radial) margin articulation. Isolated occurrences of this morphology are also seen in *Canis* and Otariidae.

151: Carpus – metacarpal II strongly overlaps III proximally (Bryant 1991): 0 – overlap small or absent (*Canis*); 1 – overlap present and substantial (*Felis*)

A lack of an overlap is plesiomorphic for Carnivormorpha. *Tapocyon*, the nimravids, and *Felis* all possess an overlap between the metacarpals. The similar morphology between the nimravids and *Felis* is reconstructed as unambiguously convergent, as opposed to the ambiguous reconstruction at node X, the feature is either attained at this node, grouping *Tapocyon* with the crown, or is independently derived in *Tapocyon* and the nimravids.

152: Carpus – metacarpal length (Van Valkenburgh 1985): 0 – metacarpal lengths are equivalent to sum of phalanges (*Vulpavus*); 1 – metacarpals are much longer than sum of phalangeal lengths (*Canis*); 2 – phalanges are longer than metacarpals (Otariidae)

Relatively short metacarpals are plesiomorphic for Carnivoramorpha. Elongation is seen independently in *Canis*, *Daphoenus* and a *Hyaena* plus *Felis* grouping. Long phalanges are found in Otariidae.

153: Carpus – medial phalanx distal articular surface symmetry (Bryant *et al.* 1996): 0 – symmetrical (*Vulpavus*); 1 – asymmetrical (*Felis*)

A symmetrical condition is plesiomorphic for Carnivoramorpha. An asymmetrical condition first develops in *Tapocyon*, and unites this taxon with the nimravids and crown Carnivora. A reversal to a symmetrical morphology unites the Caniformia and occurs independently in *Herpestes*.

154: Carpus – proximal phalanges compressed dorsoventrally (Bryant 1991): 0 – absent (*Vulpavus*); 1 – present (*Hoplophoneus*)

A compressed proximal phalanx unites the nimravids, and occurs independently in *Nandinia* and *Felis*.

155: Carpus – lateral excavation of the medial phalanx (Bryant 1991): 0 – absent (*Vulpavus*); 1 – present (*Felis*)

Lack of an excavation is plesiomorphic for Carnivoramorpha. Its acquisition unites *Miacis uintensis* with the crown group Carnivora (node 5). This state also occurs in *Dawsonicyon*; however, due to the rarity of preserved phalanges of basal carnivoraformes, it is ambiguous if *Dawsonicyon* developed this morphology independently or if it developed at node 1, or even at the base of carnivoraformes. The two species of *Vulpavus* that preserve the medial phalanx are united by a lack of an excavation. The excavation is convergently lost in the Caniformia and *Herpestes*.

156: Femur – lesser trochanter orientation (Matthew 1909): 0 – projects posteriorly (*Didymictis*); 1 – projects medially (*Vulpavus*)

The creodonts are united by a posteriorly directed lesser trochanter. This character has an ambiguous reconstruction at the base both Carnivoramorpha. A monophyletic subset of basal Carnivoraformes is characterized by a medially projecting trochanter. The earliest diverging node within Carnivoraformes for which the polarity of this character can be unambiguously reconstructed is that in which *Miacis uintensis* is united with crown Carnivora (node 5), via a rearward projecting trochanter. There are several isolated cases of convergent acquisition of the medially projecting state above this node (i.e. *Tapocyon*, *Nandinia*, *Mephitis*, and *Ailurus*).

157: Femur – intertrochanteric crest extent (new): 0 – extends to lesser trochanter (*Didymictis*); 1 – becomes flush with shaft before reaching the lesser trochanter (*Vulpavus*)

A prominent crest is plesiomorphic for Carnivoramorpha. In basal carnivoramorphs (in which the morphology is known), with the exception of *Oödectes*, the crest becomes flush with the shaft. The feature reverts to the primitive condition several times in crown Carnivora, uniting the canids, and shared by the *Civetictis*, *Herpestes*, *Hyaena* and *Felis* clade within feliforms.

158: Femur – position of lesser trochanter relative to the third trochanter (new): 0 – third trochanter is lower (*Vulpavus*); 1 – third trochanter is roughly at the same level (*Didymictis*)

The derived morphology of a third trochanter at roughly the same level as the lesser trochanter is found only in the Viverravidae.

159: Femur – third trochanter development (new); 0 – a prominent feature that juts out from the lateral boundary of the shaft both proximally and distally (*Didymictis*); 1 – a more ‘shelf-like’ feature that is smoothly connected to the greater trochanter proximally, only jutting out from the border of the shaft distally (*Vulpavus*)

A less well-developed third trochanter is typically of most of the Ferae, with a clearly defined feature found only in the Viverravidae and *Hyaenodon*.

160: Femur – supracondylar tuberosities (new): 0 – absent (*Vulpavus*); 1 – presence of two or more raised tuberosities just proximal to the condyles of the femur on the posterior shaft (*Canis*)

Absence of supracondylar tuberosities is plesiomorphic for Carnivoramorpha. The tuberosities are independently acquired in *Procyonodictis* and clade containing the canids and *Daphoenus*. No taxon in this study possesses a single tuberosity.

161: Femur – height of greater trochanter relative to head of femur (new): 0 – greater trochanter is higher or sub-equal (*Vulpavus*); 1 – greater trochanter is lower than head of femur (*Ursus*)

Among carnivoramorphans, only *Ursus* has a greater trochanter lower than the femoral head.

162: Femur – medial condyle morphology (new): 0 – proximal edge of the articular surface of condyles are flush with the shaft, due to the lack of development of a condylar neck (*Vulpavus*); 1 – proximal edge of the articular surface of condyles are not flush with the shaft, due to the development of a condylar neck (*Canis*)

It is plesiomorphic for the Ferae to have condyles that are not far separated from the shaft proximally. At the node uniting “*Miacis*” *uintensis* with more crownward Carnivoramorpha (node 5), the articular surface transforms to be separated from the shaft. This reverts to the primitive condition three times within the clade; the only synapomorphic

re-appearance of the primitive condition groups arctoids to the exclusion of *Gulo*.

163: Femur – lesser trochanter development (new): 0 – strong, prominently projecting feature (*Vulpavus*); 1 – small, barely more than a small bump or ridge on the shaft (*Ursus*)

The lesser trochanter is strong plesiomorphically for Carnivoramorpha. A reduction of the feature groups feliforms with the exception of *Herpestes*, arctoids with the exception of *Gulo*, and the morphology also independently occurs in *Canis*.

164: Femur – greater trochanter broadest surface, orientation (new): 0 – faces laterally (*Vulpavus*); 1 – faces posteriorly (*Canis*)

A posteriorly facing greater trochanter is a synapomorphy of canids in this analysis.

165: Femur – ridge of bone connecting greater trochanter and head, shape (Heinrich & Rose 1997); 0 – thin and curved (*Didymictis*); 1 – thick and straight (*Vulpavus*)

In the current dataset, the thin and curved morphology is seen only in *Didymictis*.

166: Femur – patellar groove shape (Heinrich & Rose 1997): 0 – deep and narrow (*Didymictis*); 1 – wide and flat (*Vulpavus*)

A deep and narrow patellar groove on the femur is plesiomorphic for Carnivoramorpha. There are two independent acquisitions of the wide and flat morphology; one unites a subset of basal carnivoramorphs, the second unites *Tapocyon* with the crown Carnivora (node 8). Within the crown group, independent reversals group the canids and extant feliforms with the exception of *Nandinia*.

167: Femur – position of greater trochanter relative to shaft (new): 0 – greater trochanter over distal midline (*Erinaceus*); 1 – greater trochanter lateral to midline (*Didymictis*)

The greater trochanter is found over the distal midline only in the outgroup hedgehogs.

168: Tibia – tibia and fibula fusion (new): 0 – fusion present (*Erinaceus*); 1 – fusion absent (*Didymictis*)

Fusion is absent in all of the Ferae, but present in the outgroup hedgehogs (Erinaceidae).

169: Tibia – deep groove on the posterior surface of the tibia (Matthew 1909): 0 – present (*Vulpavus*); 1 – absent (*Canis*)

A deep groove on the tibia is plesiomorphic for Carnivoramorpha. This groove is lost several times independently in the crown clade: in *Canis*, arctoids, and feliforms to the exclusion of *Nandinia*.

170: Tibia – posterior bone spur on distal tibia (new): 0 – presence of a prominent bone spur on the posterior margin (*Vulpavus*); 1 – spur absent (*Nandinia*)

The absence of this bone spur unambiguously unites the crown Carnivora with the nimravids.

171: Tibia – contact of inner borders of condyles (new): 0 – in contact (*Vulpavus*); 1 – separate (*Canis*)

At the base of both Carnivoramorpha and Carnivoraformes this character is ambiguous. The crown Carnivora is united by tibial condyles that are clearly separate from one another. Carnivoraform taxa outside of the crown that preserve proximal tibia typically have the opposite condition, with the exception of *Miacis uintensis*.

172: Tibia – internal malleolus morphology (new): 0 – forms a clear and distinct well-defined point (*Vulpavus*); 1 – indistinct, forming a general extension of the medial surface of the tibia (*Civettictis*)

The well defined condition is seen in all taxa, including outgroups, with the exception of the independent occurrence of an indistinct malleolus in *Civettictis* and *Hyaena*.

173: Pes – astragalus – length of medial border of astragalus tibial trochlea (Flynn *et al.* 1988): 0 – shorter than lateral (*Erinaceus*); 1 – longer than lateral (*Vulpavus*)

All Ferae in this study have a medial border that is longer than the lateral border on the astragalus tibial trochlea; outgroups possess a shorter medial border.

174: Pes – dorsal surface of astragalus, shape (Matthew 1909): 0 – smooth (*Vulpavus*); 1 – grooved (*Canis*)

A smooth astragalus surface is plesiomorphic for Carnivoramorpha, with the acquisition of a groove serving as a synapomorphy of Carnivora, with convergent evolution of the trait in *Hyaenodon* and *Procynodictis*. A reversal to the primitive smooth state is seen in *Mephitis*.

175: Pes – astragalus – height of fibular facet (new): 0 – height subequal to length, resulting in a roughly square shaped facet (*Vulpavus*); 1 – height much less than length, resulting in a more crescent shaped feature (*Canis*).

A square shaped fibular facet of the astragalus unites the Ferae. A more compressed fibular facet develops at the node containing *Procynodictis* and Carnivora (node 6). Independent reversals to a square facet are inferred for *Hoplophoneus* and within a subset of arctoid taxa.

176: Pes – astragalus head shape when viewed dorsally (new): 0 – rounded (*Vulpavus*); 1 – flattened (*Canis*)

A rounded head is primitive for Carnivoramorpha. The evolution of a flattened astragalus head unites the canids and occurs independently in three arctoids: *Mephitis*, *Ursus* and *Gulo*.

177: Pes – height of astragalus head when viewed distally (Heinrich & Rose 1997): 0 – apex of astragalus head even with or higher than articular surface (*Didymictis*); 1 – apex of astragalus head very low, does not rise above astragalus neck (head flattened) (*Vulpavus*); 2 – apex of astragalus head rises inbetween astragalus neck and articular surface of astragalus body (*Canis*).

Creodonts have a high astragalus head. The primitive condition of this character at the base of Carnivoramorpha is ambiguous and remains so until the node containing *Procynodictis* and the crown, where we reconstruct a flattened state. Polarity is again uncertain at the base of the crown, as a median height of the head is obtained in several taxa.

178: Pes – astragalus fossa, on the lateral edge, posterior ventral quadrant (new): 0 – present (*Didymictis*); 1 – absent (*Vulpavus*)

Within the Ferae, the absence of the fossa optimizes at the base of the carnivoraforms, with ambiguous reconstructions deeper in the clade. The fossa is regained in the nimravids, arctoids, and some feliforms; however, it is not clear if this reacquisition is independent events or if it is a shared trait, depending on the optimization method (Deltran vs Acctran). In the latter reconstruction, the loss of the feature in the canids and *Nandinia* would be convergent.

179: Pes – astragalus lateral margin, anterior ventral edge expansion (new): 0 – lateral expansion present (*Vulpavus*); 1 – expansion absent, creating a much smoother margin (*Procyon*).

Primitively for Carnivoramorpha there is a process or expanded margin on the anteriolateral ventral corner of the body of the astragalus. The loss of this process unites the Caniformia and occurs independently in *Felis*. Within the Caniformia there are at least two reversals to the primitive condition.

180: Pes – astragalus head medial articulation surface extent (new): 0 – extends backwards a great distance, past the border of the sustentacular facet (*Hyaenodon*); 1 – short, does not extend past the start of the neck (*Vulpavus*).

Primitively for Carnivoramorpha the articular surface of the astragalus head extends posteriorly past the sustentacular facet. Carnivoraformes is united by the restriction of the articular surface. Within this group, *Felis* and *Hyaena* are united by the reversal to the primitive condition.

181: Pes – astragalus sustentacular facet shape (new): 0 – has clear edges, is somewhat convex, and does not extend into gully (*Vulpavus*); 1 – is more flat than convex and extends into gully (*Canis*).

Within Ferae the sustentacular facet has clearly defined edges and is convex primitively. While the exact position of the development of a flatter, more expanded facet is

ambiguous, we can reconstruct this transformation occurring no deeper than at node 5 – containing *Miacis uintensis* and crown Carnivora. Within this group two reversals are seen within the caniforms.

182: Pes – astragalus foramen (Wang 1993): 0 – present and dorsally positioned (*Vulpavus*); 1 – present and posteriorly positioned (*Hyaenodon*); 2 – absent (*Canis*).

At the base Ferae we reconstruct an astragalus foramen that is positioned posteriorly. Carnivoramorpha is united by location of this foramen dorsally; however, taxa just outside the crown Carnivora (*Tapocyon* and the nimravids) revert to a posteriorly positioned foramen. The crown clade itself is united by the loss of the foramen. This foramen is reacquired up to three separate times in Caniformia.

183: Pes – astragalus, posterior ridge for ligament attachments, presence (Wang 1993): 0 – present, high (*Vulpavus*); 1 – low or absent (*Felis*).

Primitively for Carnivoramorpha there is a large ridge on the posterior surface of the astragalus, the absence of which serves to unite the nimravids with crown carnivorans, and which possibly occurs independently in *Procynodictis*. Within Caniformia, the high ridge occurs again in *Canis* and some of the arctoids.

184: Pes – astragalus, orientation of posterior ridge for ligament attachments (Heinrich & Rose 1997): 0 – orientated at an oblique angle relative to the long axis of the astragalus trochlea (*Vulpavus*); 1 – orientated in line with the trochlea (*Canis*).

A ridge orientated at an angle to the trochlea is plesiomorphic for Carnivoramorpha. The presence of a ridge in line with the trochlea serves to unite the nimravids with crown Carnivora. There are three isolated reversals to the primitive condition within Caniformia, in *Hesperocyon*, *Ursus*, and *Gulo*.

185: Pes – astragalus-tibia articulation surface, extent (Heinrich & Rose 1997): 0 – covers entire posterior dorsal surface (*Canis*); 1 – restricted, fails to cover entire posterior dorsal surface, leaving a gap in the lateral posterior quadrant (*Vulpavus*).

Primitively in Ferae the articular surface covers the whole dorsal astragalus body. Carnivoramorpha is united by the restriction of the articulation. At the base of Carnivora the articular surface expands again.

186: Pes – astragalus border heights (Polly 1996): 0 – lateral border subequal in height to medial border (*Thinocyon*); 1 – lateral border raised relative to medial border (*Hyaenodon*); 2 – medial border higher (*Erinaceus*).

Ancestrally, the astragalus of Ferae has a lateral border that is higher than the medial border. Several taxa or clades independently acquire more equal margins, most

notably the nimravids and a subset of basal carnivorans (*Oödetes* and *Vulpavus*).

187: Pes – astragalus, cotylar fossa presence (Heinrich & Rose 1997): 0 – present (*Didymictis*); 1 – absent (*Vulpavus*).

A cotylar fossa is present on the astragalus of creodonts and *Didymictis*, with an ambiguous reconstruction at the bases of both Ferae and Carnivoramorpha. Its absence is primitive for carnivorans. This fossa occurs again, to unite nimravids and the crown taxa; with three independent reversals to a loss of the feature within the crown caniforms.

188: Pes – Calcaneus, sustentaculum position (Heinrich & Rose 1997): 0 – far from anterior border, roughly in the middle of the calcaneus (*Didymictis*); 1 – close to anterior border (*Vulpavus*).

For Ferae, the primitive condition is a sustentaculum that is close to the anterior border. *Didymictis*, a subset of feliforms, and *Canis* all possess the derived state.

189: Pes – Calcaneus, peroneal tubercle development (Heinrich & Rose 1997): 0 – weakly developed, little more than a ridge (*Didymictis*); 1 – well developed (*Vulpavus*).

Primitively for Carnivoramorpha, the peroneal tubercle is not well developed; the derived state appears independently in a subset of basal carnivorans and at crown Carnivora, with isolated reversals within the crown.

190: Pes – astragalus neck development (new): 0 – absent (lacks a clearly defined neck of astragalus) (*Erinaceus*); 1 – present (*Vulpavus*).

The primitive condition is found in the hedgehogs included in this study, with the acquisition of a well-developed neck uniting the Ferae.

191: Pes – calcaneus, cuboid facet shape (Heinrich & Rose 1997): 0 – irregularly shaped (*Didymictis*); 1 – round (*Vulpavus*).

An irregularly shaped cuboid facet of the calcaneus is plesiomorphic for Carnivoramorpha, with most carnivorans sharing a round facet. There are at least four independent, isolated reversals to the primitive state within Carnivorans (three of these within the crown Carnivora).

192: Pes – calcaneus, cuboid facet orientation (new): 0 – angled dorsally (*Vulpavus*); 1 – in planes other than dorsal (*Didymictis*).

A facet with no dorsally oriented component is primitive for Carnivoramorpha; the derived condition groups the *Vulpavus* species, and occurs within some arctoids and *Nandinia* independently.

193: Pes – calcaneus, fibular facet (Flynn & Galiano 1982): 0 – present (*Didymictis*); 1 – absent (*Vulpavus*).

A contact between the fibula and calcaneus is primitive for Carnivoramorpha, with the derived condition uniting Carnivoraformes. *Herpestes* has a reversal to the primitive condition.

194: Pes – calcaneus –dorsal facet morphology (new): 0 – smooth (*Vulpavus*); 1 – clearly defined, sharp corner (rather than a smooth curve) (*Canis*)

A smooth facet is primitive for Carnivormorpha. A sharply angled facet unites Carnivora. This condition reverts independently in a subset of the arctoids and *Herpestes*.

195: Pes – cuboid, contact with metatarsal V (Bryant 1991): 0 – small (less than 40%) articular surface for metatarsal V (*Dinictis*); 1 – large, articular surface for metatarsal V at least 40% of distal surface (*Canis*)

Outgroup taxa to the Carnivoramorpha have a small articular surface for the 5th metatarsal. Basal carnivormorphans show an expanded articular surface (i.e. in *Didymictis* and *Vulpavus*). However, it is ambiguous if this was a shared change inherited from the common ancestor of these taxa, or if the morphology was derived independently in each. The small articular surface also groups *Miacis uintensis* with crown Carnivora. Within the crown Carnivora, there is the acquisition of a large articular surface uniting Caniformia.

196: Pes – cuboid shape (Heinrich & Rose 1997): 0 – relatively rectangular (*Didymictis*); 1 – wider proximally than distally (*Vulpavus*)

The first node within Carnivoramorpha for which we can unambiguously reconstruct the ancestral condition is the base of the Carnivoraformes, which optimizes with a cuboid having a wider proximal portion; however, this state could be primitive for the whole taxon sample, as reconstructions are ambiguous below this node. *Didymictis* has a rectangular cuboid.

197: Pes – cuboid, tubercle for the long plantar ligament, position (Heinrich & Rose 1997): 0 – distal to the ectocuneiform articulation facet (*Didymictis*); 1 – even with the ectocuneiform articulation facet (*Vulpavus*)

As with the previous character, the reconstruction of ancestral states for this character is uncertain below the Carnivoraformes clade, where we reconstruct a primitive state in which the tubercle for the long plantar ligament is even with the ectocuneiform articulation facet.

198: Pes – cuboid/astragalus contact (Matthew 1909): 0 – present (*Thinocyon*); 1 – absent (*Vulpavus*)

The creodonts in this study share the presence of a contact between the cuboid and astragalus. This contact is absent in all Carnivoramorpha.

199: Pes – navicular height (new): 0 – height less than width (*Vulpavus*); 1 – height roughly equal to or greater than width (*Canis*)

Primitively for Carnivoramorpha the navicular is wider than it is tall. In “*Miacis*” *uintensis* and *Canis* the two dimensions are subequal.

200: Pelvis – ilium, anterior expansion (new): 0 – not expanded (*Felis*); 1 – expanded dorsoventrally (*Canis*)

Primitively for Carnivoramorpha the anterior ilium is not dorsoventrally expanded; however in *Canis*, *Ursus*, *Hyaena*, and *Civettictis* a clear expansion is seen.

201: Pelvis – ischial spine position (Heinrich & Rose 1997): 0 – located just posterior of the border of the acetabulum (*Didymictis*); 1 – far posterior from acetabulum (*Vulpavus*); 2 – spine absent (*Erinaceus*)

The spine is absent in the outgroup erinaceomorphs. In Ferae a spine located far from the acetabulum is primitive, with all known viverravids sharing the condition of a spine close to the acetabulum. Within Carnivora there are two independent acquisitions of the derived morphology: *Canis* and a subgroup of Arctoidea.

202: Pelvis – dorsal margin of acetabulum, position (new): 0 – even with or above dorsal surface of pelvis (*Vulpavus*); 1 – ventral to dorsal surface of pelvis (*Canis*)

Primitively for Carnivoramorpha, the dorsal margin of the acetabulum is even with the dorsal surface of the pelvis. In crown carnivorans, there are three separate instances of the derived morphology: *Canis*, the clade containing *Ursus*, *Ailurus* and the pinnipeds, and all living feliforms except *Nandinia*.

203: Pelvis – angle at pubic symphysis (new): 0 – ‘U’ like (*Canis*); 1 – ‘V’ like (*Felis*)

The primitive morphology for Carnivoramorpha is to have a ‘V’ like pubic symphysis. *Canis* and a subgroup of feliforms independently obtain a ‘U’ like pubic symphysis.

204: Pelvis – ilium, anterior region morphology (new) 0 – broad and flat (*Canis*); 1 – divided by a distinct ridge running antero-posteriorly (*Vulpavus*)

The Ferae are united by the development of a ridge on the ilium. This ridge is lost to unite the crown Carnivora, with a reversal seen in *Hesperocyon*.

205: Pelvis – ilium, ventral surface morphology (Matthew 1909): 0 – broad and flat (*Thinocyon*); 1 – narrow (*Vulpavus*)

A broad and flat ventral surface of the ilium is primitive for Carnivoramorpha. A reduction of this surface to a narrow, blade-like morphology groups the carnivoraformes. A reversal to the primitive condition is seen in all included arctoids, with the exception of *Ursus*.

206: Atlas – posterior transverse foramen position (new): 0 – dorsal to the transverse processes (*Canis*); 1 – in line with or ventral to the transverse processes (*Felis*)

Primitively for Carnivoramorpha, the posterior transverse foramen is at the same level as the transverse processes. In up to three separate acquisitions (*Otarocyon* and *Canis*, pinnipeds and *Ailurus*) the foramen is located dorsal to the processes.

207: Atlas – alar foramen (new): 0 – absent, only a notch is present (*Canis*); 1 – present, confluent with lateral vertebral foramen (*Herpestes*); 2 – present, separate from lateral vertebral foramen (*Procyon*)

Primitively in Carnivoramorpha the two foramina are located in a shared fossa. In *Dinictis*, *Otaryocyon* plus *Canis*, and isolated arctoids we find the loss of the foramen, with only a notch present. In *Procyon* and *Otariidae* the foramen is present, but not within the same fossa as the lateral vertebral foramen.

208: Atlas – transverse processes, orientation (new): 0 – projects at right angle from the body (*Canis*); 1 – extends posteriorly at an acute angle to the body (*Nandinia*)

Primitively for Carnivoramorpha, the transverse processes of the atlas extend outwards at a right angle from the body. Feliforms are united by orientation of the processes backwards, with a reversal in *Felis*. *Ursus* has independently attained the same morphology as most of the feliforms.

209: Atlas – ventral arch length (Gaubert 2005): 0 – equal to or shorter than dens of axis (*Canis*); 1 – longer than dens of axis (*Civettictis*)

In the current study, this is an autapomorphy of *Civettictis*.

210: Axis – body length (new): 0 – roughly as long as it is wide (*Vulpavus*); 1 – elongated relative to its width (*Felis*)

The primitive state within Carnivoramorpha for this character is an axis that is roughly as long as it is wide. The polarity of this character is uncertain at the base of carnivoraforms, but feliforms are united by an elongated axis.

211: Cervical vertebrae – keel (new): 0 – large ventral keel present (*Nandinia*); 1 – ventral keel absent (*Dinictis*)

Primitively, carnivoramorphans cervical vertebrae have a large ventral keel. Loss of the keel unites the nimravids. Within crown Carnivora, the keels are independently lost in *Otarocyon*, *Felis*, and arctoids (with the exception of pinnipeds).

212: Cervical vertebrae – spinous processes, size (new): 0 – large (*Canis*); 1 – small (*Felis*)

Small spinous processes on the cervical vertebrae are primitive for Carnivoramorpha. The derived condition unites the canids, and arises independently in *Gulo*, *Nandinia* and *Herpestes*.

213: Cervical vertebrae – dorsal lateral margin shape (new): 0 – concave (*Oödetes*); 1 – convex (*Felis*)

The derived condition of convex lateral margins of the dorsal cervical vertebrae is seen to arise independently in *Nandinia* and *Felis*.

214: Lumbar vertebrae – ‘wrapping’ interlocking zygapophyses (Mellet 1977): 0 – present (*Hyaenodon*); 1 – absent (*Vulpavus*)

Interlocking zygapophyses, in which the postzygapophyses wrap around the prezygapophyses of the anterior vertebra, is an autapomorphy of *Hyaenodon* in the present study sample.

215: Sacrum – size compared to pelvis (new): 0 – small, does not reach border of acetabulum (*Canis*); 1 – large, reaches border of acetabulum (*Felis*)

Primitively within Carnivoramorpha the sacrum is large compared to the pelvis. A size reduction unites the canids, and occurs independently in *Mephitis* and *Hyaena*.

216: Sacrum – neural spines (new): 0 – clear and distinct from one another (*Nandinia*); 1 – fused to one another, appearing as one long keel (*Canis*); 2 – spines very small, hardly more than small bumps on the sacrum (*Ursus*)

The primitive condition of this character in Ferae as a whole is uncertain, but the primitive condition for carnivoraforms is ‘spines clear and distinct from one another’. Within this clade, *Canis*, a subgroup of arctoids, and *Hyaena* have spines fused to one another. The almost complete absence of spines unites *Ursus* and *Ailurus*.