



Dogs, cats, and kin: A molecular species-level phylogeny of Carnivora

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ABSTRACT

Phylogenies underpin comparative biology as high-utility tools to test evolutionary and biogeographic hypotheses, inform on conservation strategies, and reveal the age and evolutionary histories of traits and lineages. As tools, most powerful are those phylogenies that contain all, or nearly all, of the taxa of a given group. Despite their obvious utility, such phylogenies, other than summary 'supertrees', are currently lacking for most mammalian orders, including the order Carnivora. Carnivora consists of about 270 extant species including most of the world's large terrestrial predators (e.g., the big cats, wolves, bears), as well as many of man's favorite wild (panda, cheetah, tiger) and domesticated animals (dog, cat). Distributed globally, carnivores are highly diverse ecologically, having occupied all major habitat types on the planet and being diverse in traits such as sociality, communication, body/brain size, and foraging ecology. Thus, numerous studies continue to address comparative questions within the order, highlighting the need for a detailed species-level phylogeny. Here we present a phylogeny of Carnivora that increases taxon sampling density from 28% in the most detailed primary-data study to date, to 82% containing 243 taxa (222 extant species, 17 subspecies). In addition to extant species, we sampled four extinct species: American cheetah, saber-toothed cat, cave bear and the giant short-faced bear. Bayesian analysis of cytochrome *b* sequences data-mined from GenBank results in a phylogenetic hypothesis that is largely congruent with prior studies based on fewer taxa but more characters. We find support for the monophyly of Carnivora, its major division into Caniformia and Feliformia, and for all but one family within the order. The only exception is the placement of the kinkajou outside Procyonidae, however, prior studies have already cast doubt on its family placement. In contrast, at the subfamily and genus level, our results indicate numerous problems with current classification. Our results also propose new, controversial hypotheses, such as the possible placement of the red panda (Ailuridae) sister to canids (Canidae). Our results confirm previous findings suggesting that the dog was domesticated from the Eurasian wolf (*Canis lupus lupus*) and are congruent with the Near East domestication of the cat. In sum, this study presents the most detailed species-level phylogeny of Carnivora to date and a much needed tool for comparative studies of carnivoran species. To demonstrate one such use, we perform a phylogenetic analysis of evolutionary distinctiveness (EDGE), which can be used to help establish conservation priorities. According with those criteria, and under one of the many possible sets of parameters, the highest priority Carnivora species for conservation of evolutionary diversity include: monk seals, giant and red panda, giant otter, otter civet, Owston's palm civet, sea otter, Liberian mongoose, spectacled bear, walrus, binturong, and the fossa.

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1. Introduction

Detailed species-level phylogenies represent the *sine qua non* for hypothesis testing in comparative biology (Felsenstein, 1985; Harvey and Pagel, 1991). Particularly valuable are phylogenies that sample taxa densely, are well resolved, and contain estimates of

the branching history of the tree, such as branch lengths, in addition to revealing the interrelationships of species. Such phylogenies are high-utility tools that can be used to test evolutionary hypotheses, reveal coevolutionary histories of multiple traits, estimate ages of lineages and their biogeographical histories, and serve as tools for conservation, to name but a few of their uses. Despite their obvious utility, and the availability of data on GenBank, the most species-rich primary-data phylogenies available for most higher-level taxa (such as orders) within mammals contain only a small portion of the known extant species. This has sparked the reconstruction of consensus phylogenies using supertree methods

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(Bininda-Emonds, 2005; Cardillo et al., 2004; Jones et al., 2002; Price et al., 2005) that stitch together many smaller phylogenies and/or taxonomies to provide a best-guess hypothesis for higher-level taxa. As useful as supertrees have proved to be (Bininda-Emonds, 2005; Bininda-Emonds et al., 2003) they are, however, constrained by the available input data, and thus the resulting trees often have relatively low resolution, with a high number of species placed without quantitative phylogenetic estimates (i.e., derived directly from taxonomy), and typically lacking accurate estimates of branch lengths. Therefore, it remains an urgent priority to provide more detailed primary phylogenies for mammals, and other organisms. Here we present a near species-complete phylogeny of Carnivora that increases taxon sampling density from 28% in the most detailed primary-data study to date (Flynn et al., 2005) to 82%.

The order Carnivora consists of about 270 extant species that include many of the world's top terrestrial predators (e.g., cheetah, lion, leopard, tiger, hyena, wolf), man's favorite pets (dog, cat), and iconic wild animals (e.g., panda, polar bear, brown bear). Carnivores are highly diverse ecologically, having occupied all continents and all major habitat types on the planet and being diverse in traits such as sociality, communication, body/brain size, feeding ecology, etc. Thus, studies have addressed comparative questions within the order, such as the evolution of sociality (Dalerum, 2007), brain size (Finarelli, 2008; Finarelli and Flynn, 2007; Wroe and Milne, 2007), metabolic rate (Munoz-Garcia and Williams, 2005), and potential coevolution of such traits. Furthermore, the timing and the history of domestication of the cat and, especially the dog (first domesticated animal (Leonard et al., 2002)), have played a major role in the foundation of evolutionary theory (Darwin, 1859) as well as in understanding the origin and cultural transition of modern man (Savolainen et al., 2002). Clearly, a detailed species-level phylogeny will provide a tool that can further advance many types of studies.

Carnivoran species, both as top predators and as highly diverse, charismatic, and 'popular' animals also play an important role in conservation. As is true of mammalian species worldwide, many carnivores are experiencing population decline, some are currently at the brink of extinction (e.g., Falkland island fox, Caribbean monk seal, sea mink, Japanese sea lion) while many more are listed as in critical danger (e.g., Mediterranean monk seal, red wolf, Darwin's fox, Malabar civet, Iberian lynx, and the California channel island fox) (<http://www.iucnredlist.org/>). Certainly, maintaining biodiversity at the top trophic level is an important task, and understanding the phylogenetic relationships among, and within, species can aid in conservation decisions where the aim is to maximize representation of not only species, but of phylogenetic diversity (Faith, 1992, 2007; Redding and Mooers, 2006; Isaac et al., 2007; Steel et al., 2007; Helmus et al., 2007; Graham and Fine, 2008).

Carnivora has been divided into two superfamilies, Caniformia (dog-like carnivores) and Feliformia (cat-like carnivores). Caniformia is, traditionally, further divided into two infraorders Canoidea (or Cynoidea) that consist of Canidae (dogs and relatives) and Arctoidea which includes Ursidae (bears), Procyonidae (raccoons, coatis, and relatives), Mephitidae (skunks), Mustelidae (weasels, otters, and relatives), Otariidae (fur seals), Odobenidae (walrus), and Phocidae ('true' seals). Feliformia consists of the families Felidae (cats), Hesperstidae (mongooses), Hyaenidae (hyenas), Pliodontidae (linsangs), Nandiniidae (African palm civet), and Viverridae (genets, civets, and binturong). Recent phylogenetic studies, however, often differ in the interrelationships among families so that suprafamilial classification remains unstable both within Caniformia and Feliformia (see Section 4).

As data continue to accumulate from various sources (morphology, nuclear and mitochondrial DNA, behavior, fossils, etc.) certain

high-level clades tend to be conflicted, while others are repeatedly supported by independent datasets. The latter form the backbone of current knowledge, clades that have withstood many tests and can essentially be considered as 'known' or as benchmark clades by which novel phylogenetic results can be judged (Agnarsson and May-Collado, 2008; May-Collado and Agnarsson, 2006). Here, we use the single gene for which data are available for majority of mammals, cytochrome *b*, to provide a near complete species-level phylogeny of Carnivora. The record of several strongly supported high-level clades from prior studies serves to assure us that the results 'make sense'—a single-gene phylogeny that fails to recover many 'known' clades cannot be expected to represent a good working phylogenetic hypothesis at any level (May-Collado and Agnarsson, 2006; May-Collado et al., 2007; Agnarsson and May-Collado, 2008). In contrast, a phylogeny that captures known clades may also advance our understanding of relationships among species and clades that remain in dispute, or that have not yet been tested.

The main conflicts in Carnivora phylogeny surround the interrelationships among families and some lower taxonomic groups, both within Caniformia and Feliformia. For instance, the placements of Canidae, Felidae, Ursidae, and of the red panda, have been continuously disputed with each new phylogenetic study. A series of studies, using a variety of data, have been designed in an attempt to clear these higher-level conflicts, or to address more detailed species-level relationships among a subclade of Carnivora (Arnason et al., 2007; Barycka, 2007; Gaubert and Begg, 2007; Higdson et al., 2007, 2008; Koepfli et al., 2007, 2008; Krause et al., 2008; Pages et al., 2008; Patou et al., 2008). These prior studies have included a fraction of the species diversity within Carnivora, with the largest analysis to date including only about 28% of the known species diversity (76 species) (Flynn et al., 2005). Considering the known importance of dense taxon sampling for phylogenetic accuracy (Agnarsson and May-Collado, 2008; Heath et al., 2008a,b; Hedtke et al., 2006) it is clear that a more complete taxon sampling is desirable.

In this study we propose a phylogenetic hypothesis at the species-level for Carnivora including 222 extant species (out of 270 spp.) and several subspecies, along with four extinct species. This represents about 82% of the extant carnivoran species described to date. The phylogeny is based on a Bayesian analysis of *cytb* sequences, a marker that has proved to be reliable for mammals (Agnarsson and May-Collado, 2008). We evaluate our results based on the recovery of well established 'benchmark clades' and discuss the implications and potential uses of the new phylogeny for classification, conservation, and comparative biology.

2. Materials and methods

Cytochrome *b* sequences were downloaded from GenBank for 243 carnivoran taxa (see Table 1 for accession numbers), including 222 extant species, 17 subspecies, and four extinct species: two cats (a saber-toothed cat, *Homotherium serum*, and American cheetah *Miracinonyx trumani*), and two bears (cave bear, *Ursus spelaeus* and giant short-faced bear, *Arctodus simus*). As outgroups we selected 13 species of Perissodactyla and both extant species of Pholidota (pangolins), the putative sister group of Carnivora (Arnason et al., 2008; Nishihara et al., 2006). Because missing data can cause problems in phylogenetic reconstruction, we created two data matrices; one in which all taxa with available *cytb* sequences were included (full dataset = 258 taxa) and another where taxa with less than 50% of the full *cytb* sequence length were excluded (pruned dataset = 202 taxa). The sequences were aligned in Mesquite, a trivial task given that it is a protein-coding gene with no implied gaps. The appropriate model for the Bayesian analysis

Table 1

GenBank accession numbers for taxa included in the full and pruned matrix. Extinct species are marked with a cross.

GenBank scientific name	GenBank accession number	Full matrix (n = 274)	Pruned matrix (n = 202)
Outgroups			
Perissodactyla			
<i>Ceratotherium simum</i>	Y07726	×	×
<i>Coelodonta antiquitatis</i>	DQ318533	×	×
<i>Diceros bicornis</i>	EU107377	×	×
<i>Dicerorhinus sumatrensis</i>	AJ245723	×	×
<i>Equus asinus</i>	EU257216	×	×
<i>Equus burchellii</i>	DQ470804	×	×
<i>Equus cab</i>	NC_001640	×	×
<i>Equus hemionus</i>	DQ464015	×	×
<i>Equus przewalskii</i>	DQ223534	×	×
<i>Equus neogeus</i>	EU030681	×	×
<i>Equus hydruntinus</i>	DQ464013	×	×
<i>Rhinoceros sondaicus</i>	AJ245725	×	×
<i>Hippidion saldiasi</i>	AY152859	×	×
Pholidota			
<i>Manis pentadactyla</i>	EU057637	×	×
<i>Manis tetradactyla</i>	NC_004027	×	×
Carnivora			
Feliformia			
Family Nandiniidae			
<i>Nandinia binotata</i>	AF522350	×	×
Family Viverridae			
<i>Genetta sp. schoutedeni</i>	AY241900	×	×
<i>Genetta tigrina</i>	AY241877	×	×
<i>Genetta thierryi</i>	DQ395206	×	
<i>Genetta victoriae</i>	AY241894	×	
<i>Genetta rubiginosa</i>	AY751476	×	
<i>Genetta servalina</i>	AY170115	×	
<i>Genetta poensis</i>	AY241897	×	×
<i>Genetta pardina</i>	AY397707	×	×
<i>Genetta maculata</i>	AY241912	×	
<i>Genetta johnstoni</i>	AY241892	×	×
<i>Genetta felina</i>	AF125150	×	
<i>Genetta genetta</i>	AY397700	×	×
<i>Genetta cristata</i>	AY241888	×	
<i>Genetta bourloni</i>	AY241898	×	×
<i>Genetta angolensis</i>	DQ395207	×	×
<i>Cynogale bennettii</i>	DQ683992	×	×
<i>Civettictis civetta</i>	AY170105	×	×
<i>Chrotogale owstoni</i>	AF125144	×	×
<i>Arctogalidia trivirgata</i>	AF125140	×	×
<i>Arctictis binturong</i>	AY048793	×	×
<i>Poiana richardsonii</i>	AY241891	×	×
<i>Paradoxurus jerdoni</i>	DQ683994	×	×
<i>Paradoxurus hermaphroditus</i>	AF511056	×	×
<i>Paguma larvata</i>	AB303952	×	×
<i>Hemigalus derbyanus</i>	AF125143	×	×
<i>Viverricula indica</i>	AY241890	×	×
<i>Prionodon linsang</i>	AF125141	×	
<i>Prionodon pardicolor</i>	AF511048	×	
<i>Viverra zibetha</i>	AF511047	×	×
<i>Viverra tangalunga</i>	AF511045	×	×
<i>Viverra megaspila</i>	AF511046	×	×
Family Hyaenidae			
<i>Hyaena hyaena</i>	AF511063	×	×
<i>Crocuta crocuta</i>	AY928676	×	×
<i>Parahyaena brunnea</i>	AY928677	×	×
<i>Proteles cristatus</i>	AY048792	×	×
Family Eupleridae			
<i>Cryptoprocta ferox</i>	AY928681	×	×
<i>Fossa fossana</i>	AF511062	×	×
<i>Galidia elegans</i>	AY170099	×	×
<i>Galidictis fasciata</i>	AY170100	×	×
<i>Mungotictis decemlineata</i>	AY170094	×	×
<i>Salanoia concolor</i>	AY187007	×	×
Family Herpestidae			
<i>Helogale hirtula</i>	AF522335	×	×
<i>Herpestes urva</i>	DQ519074	×	×
<i>Helogale parvula</i>	AF522333	×	×

Table 1 (continued)

GenBank scientific name	GenBank accession number	Full matrix (n = 274)	Pruned matrix (n = 202)
<i>Herpestes auropunctatus</i>	X94926	×	×
<i>Herpestes edwardsii</i>	AY170107	×	×
<i>Herpestes ichneumon</i>	EF689052	×	×
<i>Herpestes naso</i>	AF522339	×	×
<i>Herpestes javanicus</i>	DQ519072	×	×
<i>Galerella sanguinea</i>	AF522331	×	×
<i>Galerella pulverulenta</i>	AF522330	×	×
<i>Cynictis penicillata</i>	AF511060	×	×
<i>Crossarchus obscurus</i>	AF522327	×	×
<i>Crossarchus alexandri</i>	AF522326	×	×
<i>Bdeogale nigripes</i>	AY950655	×	×
<i>Bdeogale crassicauda</i>	AY950654	×	×
<i>Atilax paludinosus</i>	AF522325	×	×
<i>Suricata suricatta</i>	AY170111	×	×
<i>Rhynchogale melleri</i>	AF522344	×	×
<i>Mungos mungo</i>	AF522347	×	×
<i>Liberiictis kuhni</i>	AF522342	×	×
<i>Ichneumia albicauda</i>	AF511058	×	×
Family Felidae			
<i>Acinonyx jubatus</i>	NC_005212	×	×
<i>Catopuma temminckii</i>	AY773082	×	
<i>Felis margarita</i>	EF587036	×	
<i>Felis domesticus (silvestris catus)</i>	X82296	×	×
<i>Felis chaus</i>	EU362125	×	
<i>Felis nigripes</i>	Masuda et al. (1996)	×	
<i>Felis silvestris silvestris</i>	EF587169	×	
<i>Felis silvestris ornata</i>	EF587026	×	
<i>Felis silvestris caffra</i>	EF587025	×	
<i>Felis lybica</i>	Masuda et al. (1996)	×	
<i>Lynx canadensis</i>	AY928671	×	×
<i>Lynx rufus</i>	AY499331	×	
<i>Lynx pardinus</i>	EF689048	×	×
<i>Lynx lynx</i>	D28902	×	
<i>Leopardus tigrinus</i>	AY886752	×	
<i>Leopardus pardalis</i>	DQ469951	×	
<i>Leopardus wiedi</i>	Masuda et al. (1996)	×	
<i>Homotherium serum</i> †	DQ097176	×	
<i>Herpailurus yagouaroundi</i>	AY886751	×	
<i>Panthera leo</i>	AF384815	×	
<i>Panthera tigris tigris</i>	AF053018	×	
<i>Panthera tigris sumatrae</i>	AF053048	×	
<i>Panthera tigris corbetti</i>	AF053050	×	
<i>Panthera tigris altaica</i>	AF053039	×	
<i>Panthera pardus</i>	EF551002	×	
<i>Panthera onca</i>	EF437582	×	
<i>Neofelis nebulosa</i>	DQ257669	×	
<i>Neofelis diardi</i>	EF437579	×	
<i>Miracinonyx trumani</i> †	DQ097175	×	
<i>Prionailurus bengalensis</i>	AB210233	×	×
<i>Prionailurus viverrinus</i>	AB210239	×	×
<i>Pardofelis marmorata</i>	AY499335	×	
<i>Uncia (Panthera) uncia</i>	NC_010638	×	
<i>Puma concolor</i>	AY598487	×	×
<i>Otocolobus manul</i>	Masuda et al. (1996)	×	
<i>Oncifelis geoffroyi</i>	Masuda et al. (1996)	×	
<i>Oncifelis guigna</i>	Masuda et al. (1996)	×	
<i>Ictailurus planiceps</i>	Masuda et al. (1996)	×	
<i>Lynchailurus colocolo</i>	Masuda et al. (1996)	×	
Caniformia			
Family Ailuridae			
<i>Ailurus fulgens</i>	AM711897	×	
Family Canidae			
<i>Atelocynus microtis</i>	AF028135	×	
<i>Canis lupus pallipes</i>	AY333749	×	
<i>Canis lupus lupus</i>	AM711902	×	×
<i>Canis lupus familiaris</i>	NC_002008	×	×
<i>Canis lupus chanco</i>	NC_010340	×	×
<i>Canis simensis</i>	L29415	×	
<i>Canis rufus</i>	U47038	×	
<i>Canis mesomelas elongae</i>	AF028143	×	
<i>Canis latrans</i>	NC_008093	×	×
<i>Canis indica</i>	AY291432	×	×
<i>Canis himalayensis</i>	AY291431	×	×
<i>Canis aureus</i>	AY291433	×	×

(continued on next page)

Table 1 (continued)

GenBank scientific name	GenBank accession number	Full matrix (n = 274)	Pruned matrix (n = 202)
<i>Canis adustus</i>	AF028136	×	
<i>Chrysocyon brachyurus</i>	AF028139	×	
<i>Cuon alpinus</i>	AF028137	×	
<i>Pseudalopex sechurae</i>	AF028154	×	
<i>Pseudalopex gymnocercus</i>	AF028153	×	
<i>Pseudalopex griseus</i>	AF028152	×	
<i>Pseudalopex culpaeus</i>	AF028151	×	
<i>Pseudalopex vetulus</i>	AF028148	×	
<i>Otocyon megalotis</i>	AF028150	×	
<i>Nyctereutes procyonoides</i>	AF280070	×	
<i>Lycaon pictus</i>	AF028147	×	
<i>Dusicyon thous</i>	AF028145	×	
<i>Vulpes zerda</i>	AF028146	×	
<i>Vulpes vulpes</i>	AB292765	×	×
<i>Vulpes macrotis</i>	AF042174	×	
<i>Licalopex fulvipes</i>		×	
<i>Urocyon cinereoargenteus</i>	AF028156	×	
<i>Speothos venaticus</i>	AF028155	×	
Family Ursidae			
<i>Arctodus simus</i>	FM177762	×	
<i>Tremarctos ornatus</i>	U23554	×	
<i>Melursus ursinus</i>	U23562	×	
<i>Helarctos malayanus</i>	U18899	×	
<i>Ursus americanus</i>	L21881	×	
<i>Ailuropoda melanoleuca</i>	NC_009492	×	×
<i>Ursus americanus vancouveri</i>	AF007931	×	×
<i>Ursus americanus kermodei</i>	AF007925	×	×
<i>Ursus americanus cinnamomum</i>	AF007908	×	×
<i>Ursus americanus carlottae</i>	AF007915	×	×
<i>Ursus americanus americanus</i>	AF007934	×	×
<i>Ursus americanus altifrontalis</i>	AF007911	×	×
<i>Ursus spelaeus</i> †	AF264047	×	×
<i>Ursus maritimus</i>	NC_003428	×	×
<i>Ursus arctos</i>	U18872	×	×
<i>Ursus thibetanus ussuricus</i>	AY522430	×	×
<i>Ursus thibetanus thibetanus</i>	EF587265	×	×
<i>Ursus thibetanus mupinensis</i>	AY522429	×	×
<i>Ursus thibetanus formosanus</i>	NC_009331	×	×
<i>Selenarctos thibetanus</i>	AB020910	×	×
Family Odobenidae			
<i>Odobenus rosmarus rosmarus</i>	AJ428576	×	×
Family Otariidae			
<i>Arctocephalus forsteri</i>	X82293	×	
<i>Arctocephalus tropicalis</i>	U18456	×	
<i>Arctocephalus townsendi</i>	AM181021	×	×
<i>Arctocephalus pusillus</i>	AM181018	×	×
<i>Arctocephalus philippii</i>	AF380893	×	
<i>Arctocephalus gazella</i>	X82292	×	×
<i>Arctocephalus galapagoensis</i>	AF380900	×	
<i>Arctocephalus australis</i>	AY377329	×	×
<i>Zalophus wollebaeki</i>	AM422150	×	
<i>Zalophus californianus</i>	AM181017	×	×
<i>Phocarctos hookeri</i>	AM181019	×	×
<i>Otaria byronia</i>	AY377328	×	×
<i>Neophoca cinerea</i>	AM181020	×	×
<i>Eumetopias jubatus</i>	NC_004030	×	×
<i>Callorhinus ursinus</i>	AM181016	×	×
Family Phocidae			
<i>Phoca hispida</i>	AM181036	×	×
<i>Phoca groenlandica</i>	NC_008429	×	×
<i>Phoca fasciata</i>	AM181029	×	×
<i>Phoca caspica</i>	AM181033	×	×
<i>Phoca vitulina</i>	NC_001325	×	×
<i>Phoca sibirica</i>	NC_008432	×	×
<i>Phoca largha</i>	AM181031	×	×
<i>Hydrurga leptonyx</i>	NC_008425	×	×
<i>Halichoerus grypus</i>	NC_001602	×	×
<i>Erignathus barbatus</i>	AM181027	×	×
<i>Cystophora cristata</i>	AM181028	×	×
<i>Ommatophoca rossii</i>	AY377322	×	×
<i>Monachus schauinslandi</i>	AM181022	×	×
<i>Monachus monachus</i>	AY377327	×	×
<i>Mirounga leonina</i>	AM181023	×	×
<i>Mirounga angustirostris</i>	AY424646	×	×

Table 1 (continued)

GenBank scientific name	GenBank accession number	Full matrix (n = 274)	Pruned matrix (n = 202)
<i>Lobodon carcinophaga</i>	AM181024	×	×
<i>Leptonychotes weddellii</i>	AM181025	×	×
Family Mephitidae			
<i>Mephitis macroura</i>	DQ471833	×	
<i>Mephitis mephitis</i>	X94927	×	×
<i>Spilogale gracilis</i>	DQ471834	×	
<i>Spilogale putorius</i>	AM711898	×	×
Family Procyonidae			
<i>Bassaricyon alleni</i>	DQ660299	×	×
<i>Bassaricyon gabbii</i>	DQ660300	×	×
<i>Bassariscus astutus</i>	AF498159	×	×
<i>Bassariscus sumichrasti</i>	DQ660301	×	×
<i>Nasua narica</i>	DQ660302	×	×
<i>Nasua nasua</i>	DQ660303	×	×
<i>Potos flavus</i>	DQ660304	×	×
<i>Procyon cancrivorus</i>	DQ660305	×	×
<i>Procyon lotor</i>	NC_009126	×	×
Family Mustelidae			
<i>Vormela peregusna</i>	EF581360	×	×
<i>Taxidea taxus</i>	AF057132	×	×
<i>Pteronura brasiliensis</i>	AF057126	×	×
<i>Poecilogle albinucha</i>	EF472349	×	×
<i>Neovison vison</i>	EF689076	×	×
<i>Mustela strigidorsa</i>	EF987748	×	×
<i>Mustela sibirica</i>	EF987747	×	×
<i>Mustela putorius</i>	EF987746	×	×
<i>Mustela nudipes</i>	EF987745	×	×
<i>Mustela nivalis</i>	EF987744	×	×
<i>Mustela nigripes</i>	EF987743	×	×
<i>Mustela lutreola</i>	EF987742	×	×
<i>Mustela itatsi</i>	AB026104	×	×
<i>Mustela frenata</i>	AF498153	×	×
<i>Mustela eversmannii</i>	EF987741	×	×
<i>Mustela erminea</i>	AF457442	×	×
<i>Mustela altaica</i>	AB026100	×	×
<i>Melogale moschata</i>	AF498158	×	×
<i>Mellivora capensis</i>	EF987755	×	×
<i>Meles meles anakuma</i>	NC_009677	×	×
<i>Martes zibellina</i>	EF987753	×	×
<i>Martes pennanti</i>	AF448248	×	×
<i>Martes melampus</i>	EF987752	×	×
<i>Martes foina</i>	EF987750	×	×
<i>Martes flavigula</i>	EF987749	×	×
<i>Martes caurina</i>	L77954	×	
<i>Martes americana</i>	AF268274	×	×
<i>Lutrogale perspicillata</i>	EF472348	×	×
<i>Lutra sumatrana</i>	EF472347	×	×
<i>Lutra maculicollis</i>	AF057125	×	×
<i>Lutra lutra</i>	AF057124	×	×
<i>Lutra canadensis</i>	AF418979	×	×
<i>Lontra provocax</i>	DQ341273	×	
<i>Lontra longicaudis</i>	AF057123	×	×
<i>Lontra felina</i>	AF057122	×	×
<i>Lontra canadensis</i>	AF057121	×	×
<i>Galictis cuja</i>	EF987754	×	×
<i>Galictis vittata</i>	AF498155	×	×
<i>Ictonyx striatus</i>	AF498156	×	×
<i>Ictonyx libyca</i>	EF987739	×	×
<i>Gulo gulo</i>	NC_009685	×	×
<i>Enhydra lutris</i>	AB291077	×	×
<i>Eira barbara</i>	AF498154	×	×
<i>Arctonyx collaris</i>	AF498157	×	×
<i>Aonyx capensis</i>	AF057118	×	×
<i>Amblyonyx cinereus</i>	AF057119	×	×

was selected with Modeltest (Posada and Crandall, 1998, 2001), using the AIC criterion (Posada and Buckley, 2004) with a parsimony tree chosen as the basis for Modeltest. The best model was GTR+ Γ +I (Rodríguez et al., 1990; Yang, 1994). Bayesian analysis was performed using MrBayes V3.1.2 (Huelsenbeck and Ronquist, 2001) with settings as in May-Collado and Agnarsson (2006) and

Agnarsson and May-Collado (2008) with separate model estimation for first, second, and third codon positions.

The Markov chain Monte Carlo search for each matrix was run with four chains for 20,000,000 generations (repeated twice), sampling the Markov chain every 1000 generations, and the sample points of the first 5,000,000 generations were discarded as “burnin”.

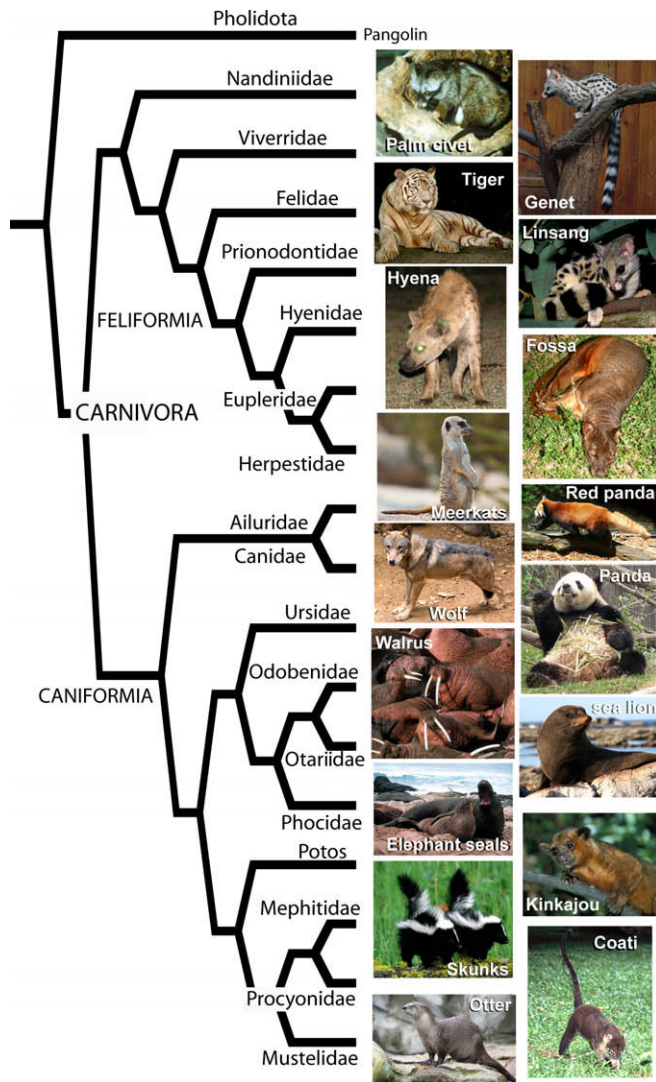


Fig. 1. Summary of relationships among carnivorous families. Photographs by M. Kuntner (tiger, hyena, fossa, panda, wolf, coati, sea lion), I. Agnarsson (otter, red panda). The following obtained with permission from ASM mammal image library: palm civet (K. Kutunidis), walrus (J.D. Haweeli), kinkajou (R.D. Lord). The following photographs are licensed under GFDL, see <http://www.gnu.org/copyleft/fdl.html>, genet (Guérin Nicolas), linsang (Alessio Marrucci), meerkat (Fir0002/Flagstaffotos). Photos of elephant seals (Jan Roletto) and skunks from public domain.

Maximum likelihood analyses were conducted in the program Garli (Zwickl, 2006), using the GTR+ Γ +I model and 200 search replications. The best tree (lowest log likelihood) from these 200 analyses (see Supplementary Fig. 1) broadly agrees with the Bayesian results. We focus our discussion on the Bayesian results as they simultaneously provide an estimate of the phylogeny, and support for it. However, we discuss the likelihood results when there are major differences with the Bayesian analysis.

May-Collado and Agnarsson (2006) showed that, in terms of the recovery of 'known' clades (benchmark clades) parsimony performed relatively poorly compared to Bayesian analyses of cytb sequences within Cetartiodactyla. Parsimony analyses were also conducted (see May-Collado and Agnarsson, 2006, for analysis parameters using parsimony), confirming our previous findings; although overall the results are quite similar, parsimony results are in greater conflict with the available external evidence (morphology, nuclear DNA, mitogenomic studies, etc.) and recover many fewer benchmark clades than Bayesian analyses (see Supplementary Fig. 1).

We use the Tuatara module (Maddison and Mooers, 2007) in the evolutionary analysis packet Mesquite (Maddison and Maddison, 2009) to assess conservation priorities for carnivorous species. We illustrate one example of such an analysis in Fig. 8. We calculated (1) evolutionary distinctiveness (ED), a measure of a species terminal branch length and its share in ancestral branches, weighted by 'global extinction' (GE) risk (=EDGE, Isaac et al., 2007) and (2) the expected terminal branch length of species, taking into account the extinction probability of all species, again weighted by extinction risk (HEDGE, Steel et al., 2007). We calculate extinction risk by translating IUCN threat categories to extinction probabilities, needed as input values in Tuatara, using the 'pessimistic' approach of Mooers et al. (2008). We note that the 'pessimistic' transformation gives relatively great weight to phylogenetic distinctiveness as all taxa are considered at some considerable risk of extinction. To allow the inclusion of 'data deficient' species we, arbitrarily, but probably conservatively, estimated their extinction risk as in between the 'least concern' and 'near threatened' categories. As emphasized by Mooers et al. (2008) results of EDGE and HEDGE analyses are sensitive to how IUCN categories are translated to extinction probabilities. However, for our purposes of showing one potential use of this phylogeny, we only illustrate one example of analyzing the data, and note that while results from other types of analyses differed in many details, the top priority species for conservation seen in Fig. 8 ranked relatively high in every analysis.

3. Results

3.1. Benchmark clades

The Bayesian analysis of the pruned dataset gave essentially identical result, differing only in terms of support values, which were typically higher than in the full analysis. Hence, we will confine most of our discussion to the Bayesian analysis including all taxa. The phylogeny recovers the monophyly of all benchmark clades (Figs. 1, 2 and Table 2). However, the Bayesian result supports a slightly modified Arctoidea and Musteloidea, due to the placement of the red panda (*Ailurus fulgens*, Ailuridae) sister to Canidae (Fig. 1). The likelihood analysis (see Supplementary Fig. 2) recovers the 'traditional' Arctoidea, but not Musteloidea, as it places the red panda sister to a clade containing all Caniformia minus Canidae. In the parsimony analysis the two long branches, red panda and kinkajou (*Potos flavus*) attract. The placement of the red panda has not been stable across prior analyses and must be considered unresolved. We find support for Carnivora, its subdivision into Caniformia and Feliformia, and for all but one of the currently recognized families within both suborders. Our Bayesian and likelihood results are incongruent with current classification at the family level only in the placement of a single species, the kinkajou which here, instead of nesting within Procyonidae, is sister to a clade containing Procyonidae, Mustelidae, and Mephitidae (Fig. 1). The parsimony results differ further, e.g., placing one cat (*Homotherium serum*) with viverrids, *Genetta felina* (Viverridae, Feliformia) with bears (Ursidae, Caniformia), by uniting the red panda and kinkajou, and placing skunks (Mephitidae) within raccoons (Procyonidae). These unlikely relationships in most cases involve taxa with notably long branches, hence potentially a result of long branch attraction. Given these issues, we do not discuss the parsimony analysis further.

3.2. Caniformia

The Bayesian results suggest a sister relationship between the red panda (*Ailurus fulgens*) and Canidae and, in turn, that

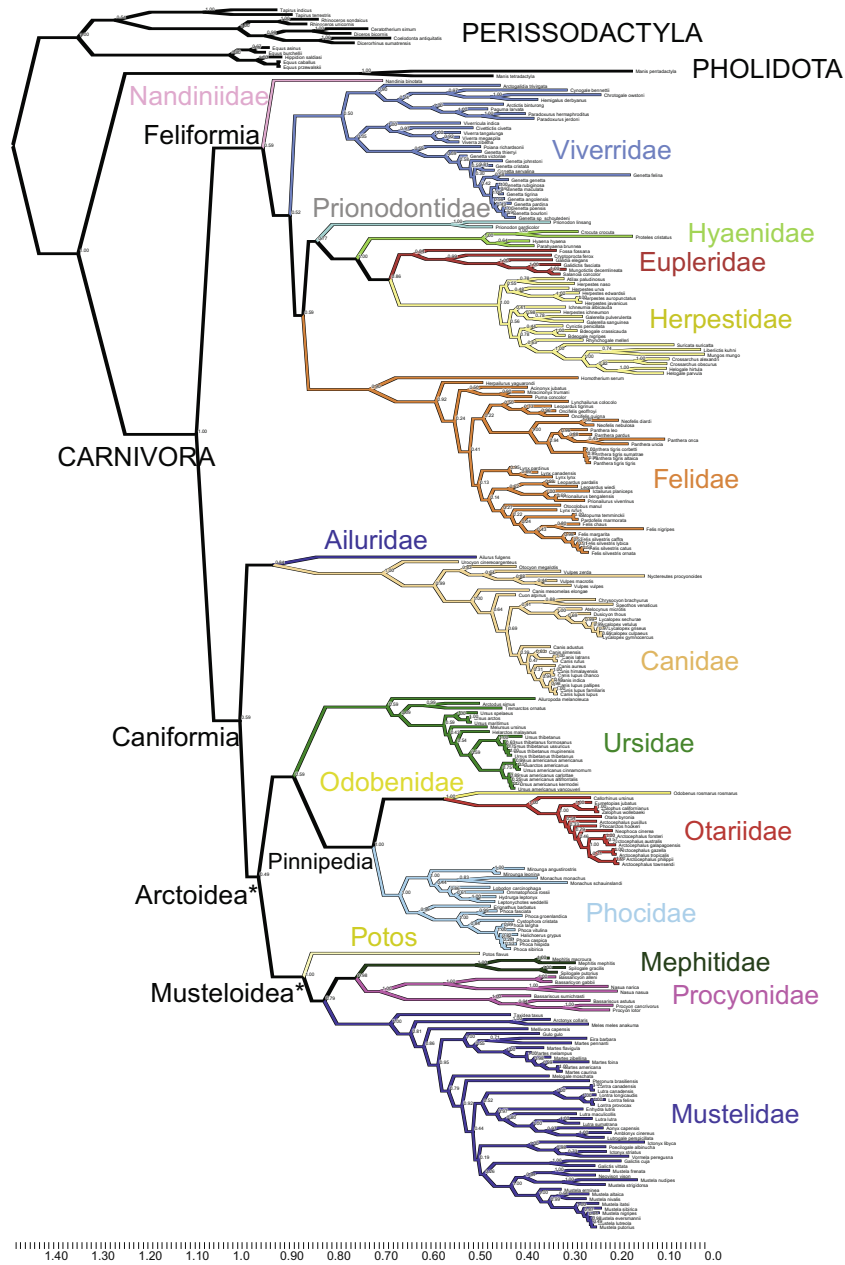


Fig. 2. Results of Bayesian analysis of the full matrix, colored by families. Branches are proportional to lengths. These results support the monophyly of all carnivoran families as currently circumscribed, except in the placement of *Potos* outside Procyonidae. They further support all benchmark clades, although with a modified Arctoidea and Musteloidea (asterisked) due to the placement of the red panda as sister to Canidae. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

this group is sister to the remaining caniforms, thus suggesting a slightly modified Arctoidea (Figs. 6 and 7). However, the likelihood analysis recovered the traditional Arctoidea (Supplementary Fig. 2). Our results also place bears (Ursidae) sister to Pinnipedia (Odobenidae—walrus, Phocidae—seals, and Otariidae—fur seals and sea lions). Within Pinnipedia the following familial relationships (Phocidae(Odobenidae + Otariidae)) was strongly supported. This Ursidae/Pinnipedia clade was sister to a well supported modified Musteloidea containing *Potos flavus* as sister to the clade (Mustelidae(Mephitidae + Procyonidae)).

3.2.1. Canidae

The monophyly of Canidae was well supported in each analysis (Fig. 6). The gray fox (*Urocyon cinereoargenteus*) was sister to the

remaining extant canids, within which two main lineages were identified, one containing bat-eared fox (*Otocyon*), racoon dog (*Nyctereutes*), and foxes (*Vulpes*), the other containing jackals, wolves, and 'dogs' (in part, in *Canis*), African wild dog (*Lycaon*), crab-eating dog (*Cerdocyon*), maned wolf (*Chrysocyon*), short-eared dog (*Atelocynus*), bush dog (*Speothos*), and the remaining 'foxes' (*Pseudalopex*). The genus *Vulpes* appears to be paraphyletic, it contains *Nyctereutes procyonoides*. The genus *Canis* is also paraphyletic with the black-backed jackal (*Canis mesomelas*) and the Dhole or Asian wild dog (*Canis alpinus*, previously *Coun*) placing outside the genus. The monophyly of the remaining *Canis* species also is very poorly supported (39% posterior probability) and *C. adustus* does not nest with *Canis* in the likelihood analysis. The domesticated dog (*Canis lupus familiaris*) is sister to the Eurasian wolf (*Canis lupus lupus*).

Table 2

Recovery and support of benchmark clades within Carnivora (numbers are posterior probability values). * refers to support for slightly modified benchmark clades, as indicated in braces. See text for details.

Benchmark clades	Full matrix	Pruned matrix
Carnivora	100	100
Caniformia	59	93
Feliformia	59*	93*
Arctoidea	49 (excluding <i>Ailuridae</i>)	49 (excluding <i>Ailuridae</i>)
Musteloidea	100 (excluding <i>Ailuridae</i>)	100 (excluding <i>Ailuridae</i>)
Mustelidae	100	100
Canidae	100	100
Mephitidae	100	100
Procyonidae	NO (100, excluding <i>Potos</i>)	NO (100, excluding <i>Potos</i>)
Pinnipedia	100	100
Otariidae	100	100
Phocidae	100	100
Ursidae	59	93
Felidae	90	100
Herpestidae	100	100
Eupleridae	54	65
Hyaenidae	100	100

3.2.2. Ursidae

Our results support a monophyletic Ursidae with the panda (*Ailuropoda melanoleuca*) as sister to the remaining bears (Fig. 6). Spectacled bear (*Tremarctos omalus*), and the extinct giant short-faced bear (*Arctodus simus*) then group strongly, to the exclusion of all remaining bears. Our results dispute the monophyly of the genus *Ursus* as the sloth bear (*Melursus ursinos*), and the sun bear (*Helarctos malayanus*) nest within it. The extinct Cave bear (*U. spelaeus*) is sister to a clade containing the polar bear (*U. maritimus*) and its sister species, the brown bear (*U. arctos*).

3.2.3. Pinnipedia—Odobenidae, Otariidae, Phocidae

The monophyly of Pinnipedia, and each pinniped family was strongly supported (Fig. 6). The Odobenidae is monotypic (walrus) and is sister to Otariidae. The subdivision of Otariidae into fur seals and sea lions is refuted. The two putative subfamilies, Arctocephalinae (*Callorhinus* and *Arctocephalus*) and Otariinae (*Eumetopias*, *Otaria*, *Zalophus*, *Noephoca*, and *Phocarctos*) were also refuted. The genus *Arctocephalus* is furthermore paraphyletic, however, only so by the weakly supported phylogenetic position of *A. pusillus* outside it. In contrast, within Phocidae, the monophyly of both subfamilies Monachinae (southern seals and monk seals: *Monachus*, *Mirounga*, *Hydrurga*, *Lobodon*, *Ommatophoca*, and *Leptonychotes*) and Phocinae (northern seals: *Phoca*, *Erignathus*, *Cystophora*, and *Halichoerus*) was strongly supported.

3.2.4. Musteloidea—Mephitidae, Procyonidae, Mustelidae

The monophyly of Musteloidea, and both Mephitidae and Mustelidae was strongly supported (Fig. 7), but not that of Procyonidae and the subfamily Potosinae, due to the placement of *Potos flavus* sister to all remaining musteloideans. Our findings refute the monophyly of the subfamily Procyoninae (*Procyon*, *Nasua*, and *Bassariscus*), instead strongly supporting a clade containing *Bassariscyon* and *Nasua*, sister to *Procyon* plus *Bassariscus*.

Current classification subdivides Mustelidae into four subfamilies, Melinae (true badgers: *Arctonyx*, *Meles*, *Mydaus*, and *Melogale*), Lutrinae (otters: *Aonyx*, *Enhydra*, *Lutra*, and *Pteronura*), Mustelinae (*Eira*, *Galictis*, *Ictonyx*, *Mustela*, *Lyncodon*, *Poecilictis*, *Poecilogale*, *Vormela*, *Martes*, and *Gulo*), Mellivorinae (honey-badger, *Mellivora*), and Taxideninae (*Taxidea*). Our results indicate that three of these subfamilies are not monophyletic (Fig. 7): (1) Melinae, due to the placement of *Melogale* sister to Lutrinae and Mustelinae, (2) Lutrinae, due to the placement of *Pteronura brasiliensis* (giant otter) also sister to both Lutrinae and Mustelinae, excluding *Melogale*. The

third subfamily, Mustelinae, was polyphyletic with its various genera scattered. In addition, the genera *Lutra*, *Ictonyx*, *Mustela*, and *Martes* were para- or polyphyletic. Our results place the monotypic Taxideninae (*Taxidea taxus*) sister to the remaining Mustelidae. The likelihood results differ mainly in the placement of the root of Mustelidae, thus suggesting quite different placement of Taxideninae (Supplementary Fig. 2).

3.3. Feliformia

Our results support the monophyly of all seven families within Feliformia (Figs. 3–5). In the Bayesian analysis the monotypic Nandiniidae (African palm civet, *Nandinia binotata*) was sister to the remaining extant Feliformia, with relationships among the remainder of cat-like carnivorans as: (Viverridae(Felidae(Prionodontidae(Hyaenidae(Eupleridae + Herpestidae))))). However, the interrelationships of families were generally poorly supported and the likelihood analysis differed, particularly in the placement of African palm civet, Prionodontidae, and Viverridae (Supplementary Fig. 2).

3.3.1. Viverridae

Within Viverridae four subfamilies have been proposed, Viverrinae (*Viverricula*, *Civettictis*, *Viverra*), Genettinae (*Genetta*, *Poiana*), Paradoxurinae (*Arctictis*, *Paguma*, *Paradoxurus*), and Hemigalinae (*Chrotogale*, *Cynogale*, and *Hemigalus*). Our results support the monophyly of Viverrinae, Genettinae, and Hemigalinae (Fig. 3). However, the small-toothed palm civet (*Arctogalidia trivirgata*, currently in Paradoxurinae) was sister to hemigalins and paradoxurins together, thus rendering Paradoxurinae paraphyletic. The interrelationships of these subfamilies was generally weakly supported and differed between the Bayesian and likelihood analyses (Fig. 3 and Supplementary Fig. 2).

3.3.2. Felidae

Within monophyletic Felidae, the extinct saber-toothed (or Scimitar-toothed) cat (*Homotherium serum*) was sister to all remaining cats (Figs. 4 and 5) in all analyses. The big cat clade contains *Panthera* and *Neofelis* species and is strongly supported. Other generally well supported clades are *Oncifelis*, *Neofelis*, and *Panthera* incl. *P. uncia*. Monophyletic but relatively weakly supported are *Prionailurus* and *Felis*, while the genera *Lynx* and *Leopardus* are paraphyletic. All results dispute the hypothesized sister group relationship of the jaguarondi (*Herpailurus yagouarundi*) and the puma (*Puma concolor*) (Masuda et al., 1996; Mattern and McLennan, 2000; Johnson et al., 2006), but the Bayesian and likelihood analyses differ in the placement of several genera on the felid tree (see Supplementary Fig. 2), for example the placement of jaguarondi, *Lynx* spp., *Octolobus*, the clade *Lynchailurus* + (*Leopardus* + *Oncifelis*), the clade *Catopuma* + *Pardofelis*, and the interrelationships of *Panthera uncia*, *onca* and *pardus*, as well as those within *Felis*. The domestic cat (*F. silvestris catus*) is always sister to the Asiatic wildcat (*F. silvestris ornata*), and these two in turn sister to the African wildcat *F. silvestris lybica*, the hypothesized ancestor of the domestic cat. The majority of clades within Felidae are poorly supported, seemingly due to the majority of felids having available only very short cytb sequences available.

3.3.3. Prionodontidae and Hyaenidae

Prionodontidae (Fig. 3) consists of only two species: banded (*P. linsang*) and spotted (*P. pardicolor*) linsangs. Within Hyaenidae, two lineages, containing two species each, were supported, the sister pair spotted hyena (*Crocuta crocuta*) and aardwolf (*Proteles cristatus*), and the pair of brown hyenas (*Hyaena hyaena* and *Parahyaena brunnea*).

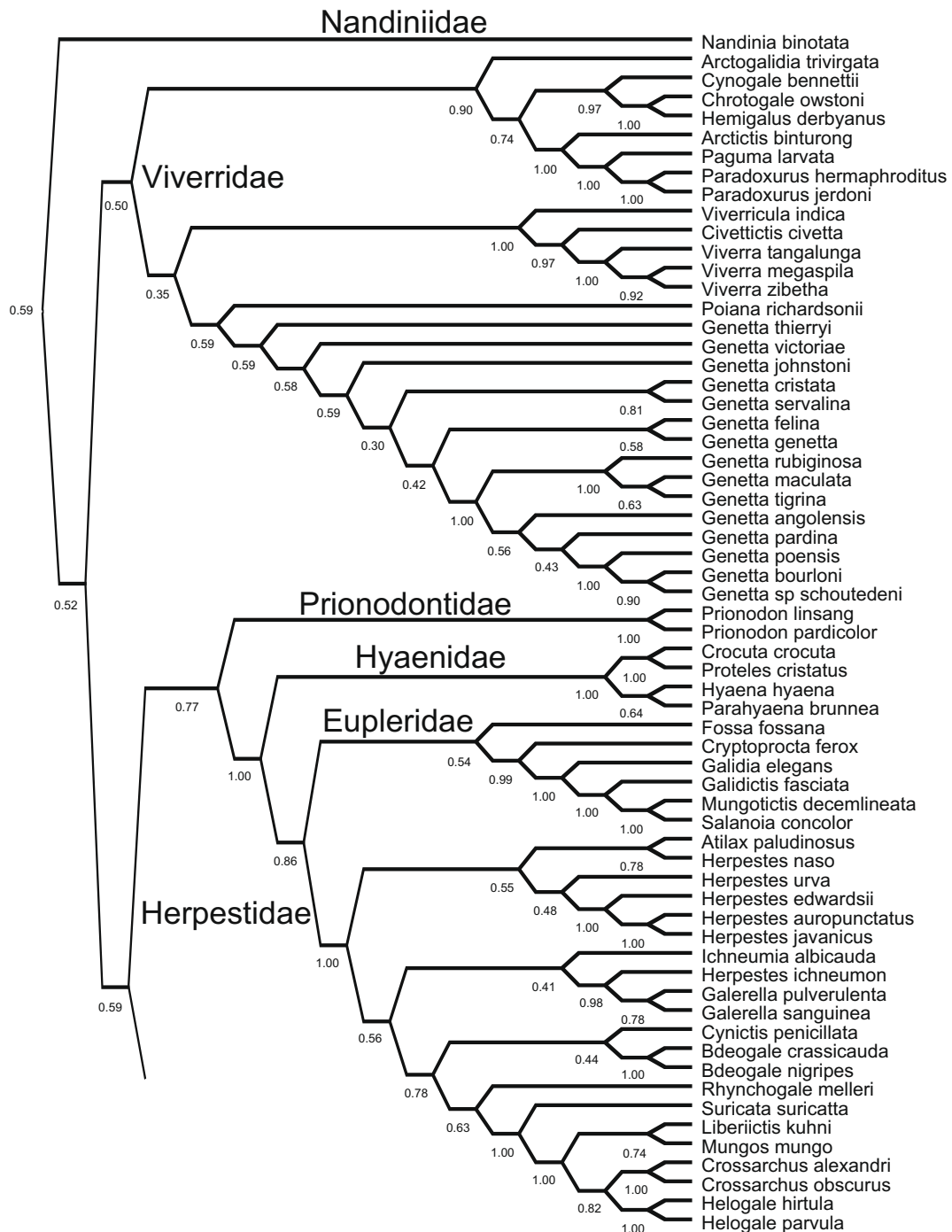


Fig. 3. Details of relationships among feliformian carnivores. Numbers are posterior probability values.

3.3.4. Eupleridae

Within Eupleridae, two subfamilies have been proposed: Galidiinae (*Galidia*, *Galidictis*, *Mungotictis*, and *Salanoia*) and Euplerinae (*Cryptoprocta* and *Fossa*). Our results support Galidiinae, but place *Cryptoprocta* sister to it so that Euplerinae is paraphyletic (Fig. 3).

3.3.5. Herpestidae

In general, the relationships within Herpestidae are rather weakly supported (Fig. 3). Our findings indicate that the genus *Herpestes* is polyphyletic. The Egyptian mongoose (*Herpestes ichneumon*) nested with *Galerella* (slender mongooses), and the long-

nosed mongoose (*H. naso*) was placed sister to the white-tailed mongoose (*Ichneumia*).

3.4. Conservation priorities

Our preliminary analysis of conservation priorities identifies a number of candidate species that, based on evolutionary distinctiveness weighted by extinction risk, may deserve special attention and conservation effort (Fig. 8). Although the ranking of species strongly depends on the parameters of choice (Mooers et al., 2008), high ranking species for conservation priorities in most analysis include: monk seals, panda, red panda, otter civet, Ow-

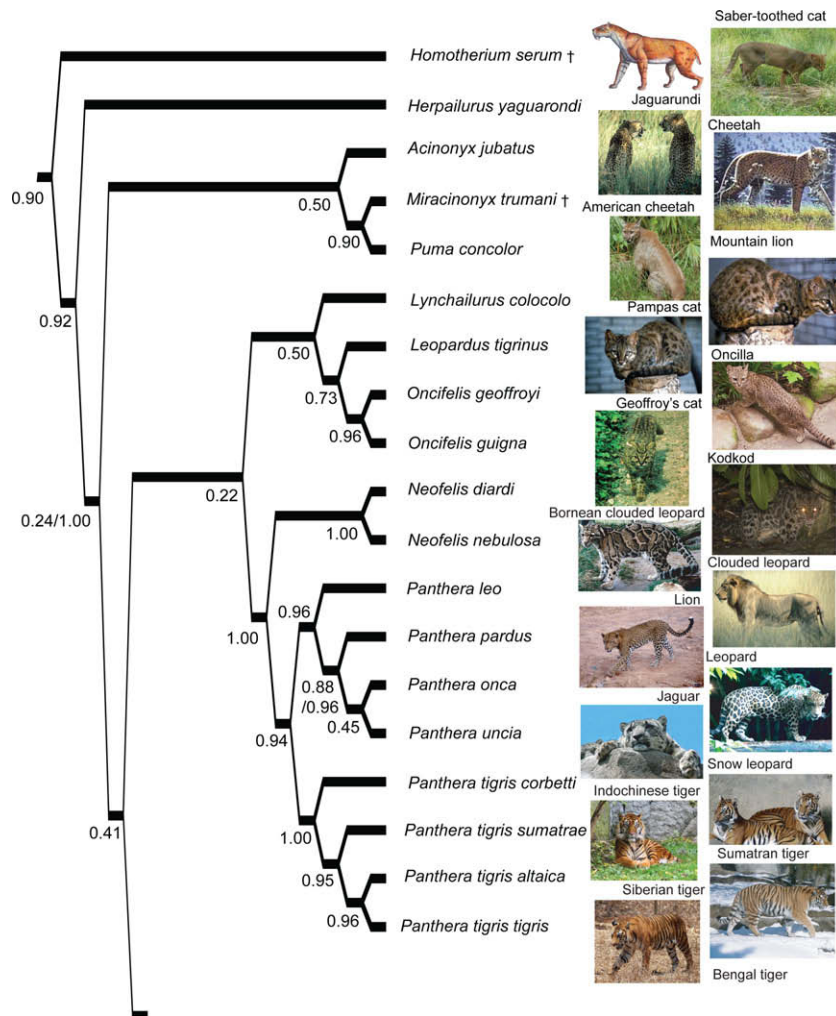


Fig. 4. Relationships among species of Felidae, see also Fig. 5. Numbers are posterior probability values with a second number representing support value in the pruned analysis, when higher than in the full analysis. Photographs by M. Kuntner (cheetah, lion, jaguar), I. Agnarsson (leopard, snow leopard). The following obtained with permission from ASM mammal image library: pampas cat and oncilla (K. Kutunidis). The following photographs are licensed under GFDL, see <http://www.gnu.org/copyleft/fdl.html>, jagouaroundi (Bodlina), Geoffroy's cat (Daf-de), Sumatran tiger (Monika Betley). Drawing of *Homotherium* by Alexis Vlachos, reproduced from Lyras and Van Der Geer (2007) with permission. Photograph of mountain lion from public domain (U.S. Fish and Wildlife). Photographs of Bornean clouded leopard (Canorus), Indochinese tiger (Kabir Bakie), Siberian tiger (MJCdetroit), Bengal tiger (Paul Mannix), licensed under the Creative Commons Attribution ShareAlike 3.0. Photograph of kodkod from Arkive (G. Acosta-Jamett).

ston's palm civet, giant otter, Liberian mongoose, fossa, black-footed cat, spectacled bear, banded palm civet, the sea otter, snow leopard, binturong, clouded leopard, and marbled polecat.

4. Discussion

Despite their obvious utility, species-complete phylogenies are lacking for most higher-level taxa (such as orders), regardless of the organism. We proposed a phylogenetic hypothesis placing 222 out of the 270 extant species of Carnivora, in addition to 17 subspecies and four extinct species, based on sequences of the cytochrome *b* mitochondrial gene. While we anticipate that future studies using more character data will likely refute some of our findings, the current phylogeny overall agrees with results that have been most stable in previous studies based on various data (e.g., Finarelli and Flynn, 2007) and thus represents a useful tool for comparative studies, and a guide to carnivoran classification.

4.1. Benchmark clades

We found strong support for the monophyly of all benchmark clades, although the Bayesian analysis recovered a slightly modi-

fied Arctoidea due to a novel placement of the red panda as sister to canids (Figs. 1 and 2). In addition, our results support the sister relationship between Carnivora and Pholidota. The recovery of all (likelihood), and all but one (Bayesian) benchmark clades gives credibility to our results in general. Clearly, the signal present in *cytb* agrees well, overall, with the most robustly supported higher-level clades that prior studies tend to agree upon (e.g., Finarelli and Flynn, 2007). Thus, it seems reasonable to assume that the novel results presented here, in particular the detailed patterns of relationships among carnivoran species represent a useful working hypothesis. Our analysis of a pruned matrix where taxa with short sequences were removed indicates that low support for placement of species is often a result of missing data (short sequences). Given the high information content in *cytb* and ease of amplification, obtaining complete *cytb* sequences for all carnivorans is an obvious priority.

4.2. Caniformia

The monophyly of Caniformia is uncontroversial and is here supported (Figs. 1, 2, and 6). Within Caniformia relationships among families have been unstable in prior studies (Flynn and

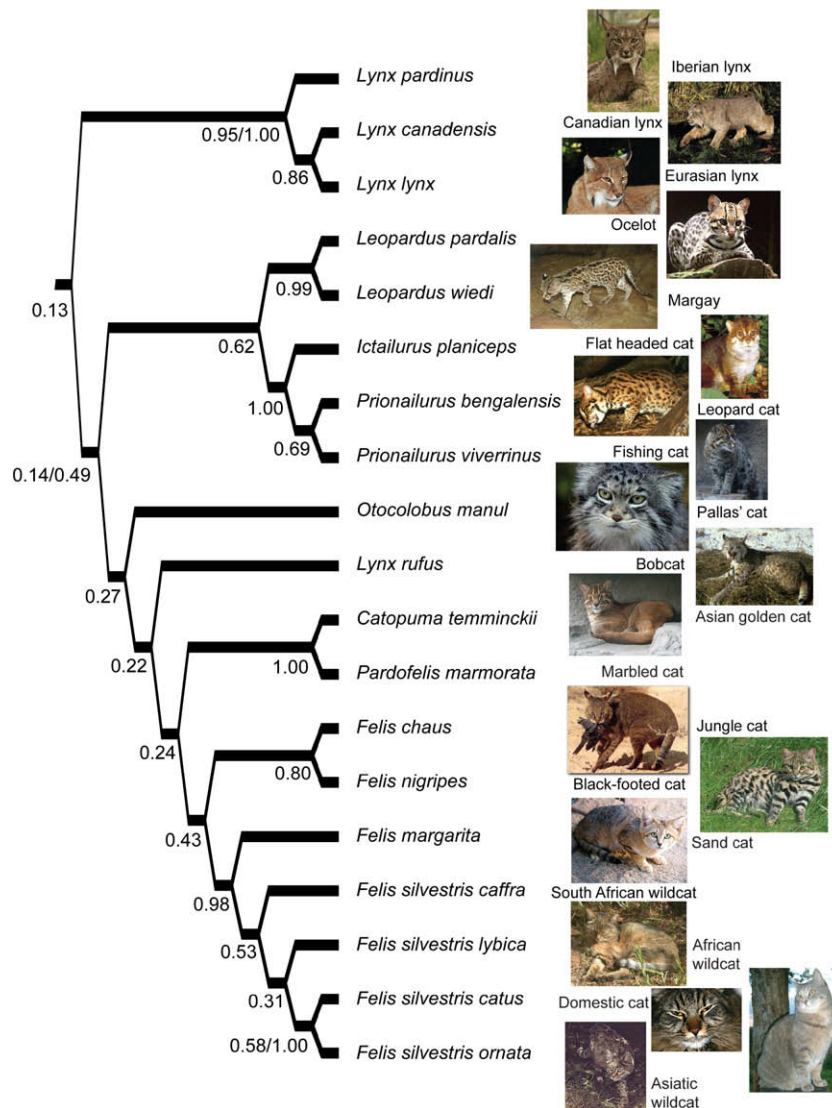


Fig. 5. Relationships among species of Felidae, continued from Fig. 4. Numbers are posterior probability values with a second number representing support value in the pruned analysis, when higher than in the full analysis. Photographs by M. Kuntner (leopard cat, domestic cat). The following images are licensed under the Creative Commons Attribution ShareAlike 2.5–3.0: Iberian lynx (Programa de Conservación Ex-situ del Lince Ibérico www.lynxexsitu.es), fishing cat (http://en.wikipedia.org/wiki/File:Prionailurus_viverrinus.jpg), Asian golden cat (OpenCage), black-footed cat (Zbyszko), Creative Commons Attribution 3.0 Unported License; Eurasian lynx (Michael Gäbler), Creative Commons Attribution 2.0: ocelot (Ana Cotta), Pallas' cat (ScottMiddell), GNU Free Documentation License: flat headed cat (http://en.wikipedia.org/index.php?title=Image:Prionailurus_planiceps.JPG#file), Asiatic wildcat, African wildcat (Sonelle). The photograph of jungle cat is not copyrighted (GorillazFanAdam). Photographs of Canadian lynx (Erwin and Peggy Bauer, U.S. Fish and Wildlife Service), margay (Ltshears), bobcat (U.S. Fish and Wildlife Service) and sand cat (DocTaxon) are from public domain.

Nedbal, 1998; Flynn et al., 2000, 2005; Yu et al., 2004; Wesley-Hunt and Flynn, 2005; Goswami, 2006; Koepfli et al., 2006; Finarelli and Flynn, 2007). Our Bayesian results challenge for the first time the monophyly of Arctoidea placing the red panda (Ailuridae) sister to canids (Fig. 6). Prior studies place Ailuridae within Arctoidea, however, the placement of Ailuridae has varied considerably in previous studies (e.g., Flynn and Nedbal, 1998; Flynn et al., 2000, 2005; Delisle and Strobeck, 2005; Goswami, 2006), and was method dependent in this study. Thus we may still regard its phylogenetic affinities as unsettled.

Arnason et al. (2007) using complete mitogenomic data highlights 'a gradually established molecular understanding' referring to the sister relationship between Musteloidea and Pinnipedia (to the exclusion of Ursidae). This relationship has also been supported by other lines of evidence including nuDNA alone (e.g., Sato et al., 2006; Ledje and Arnason, 1996a,b; Yu et al.,

2004), morphology and molecular data (e.g., Dragoo and Honeycutt, 1997; Bininda-Emonds et al., 1999), morphological data alone, (e.g., Wolsan, 1993; Bininda-Emonds and Russell, 1996), mtDNA alone (e.g., Zhang and Ryder, 1996), and combined nuclear and mitochondrial DNA (e.g., Flynn and Nedbal, 1998; Flynn et al., 2000). Nevertheless, these studies have only provided weak support for this clade. Our results, in contrast, strongly support the more traditional sister relationship between Ursidae and Pinnipedia (to the exclusion of Musteloidea, Fig. 6), as most morphological studies have suggested (e.g., Berta and Ray, 1990; Flynn and Nedbal, 1998). This arrangement has been weakly supported by combined morphological and mtDNA data (Vrana et al., 1994), and mtDNA alone (e.g., Davis et al., 2004; Lento et al., 1995; Delisle and Strobeck, 2005). However, our study is the first to strongly support this clade, a result that may well be attributable to the dense taxon sampling.

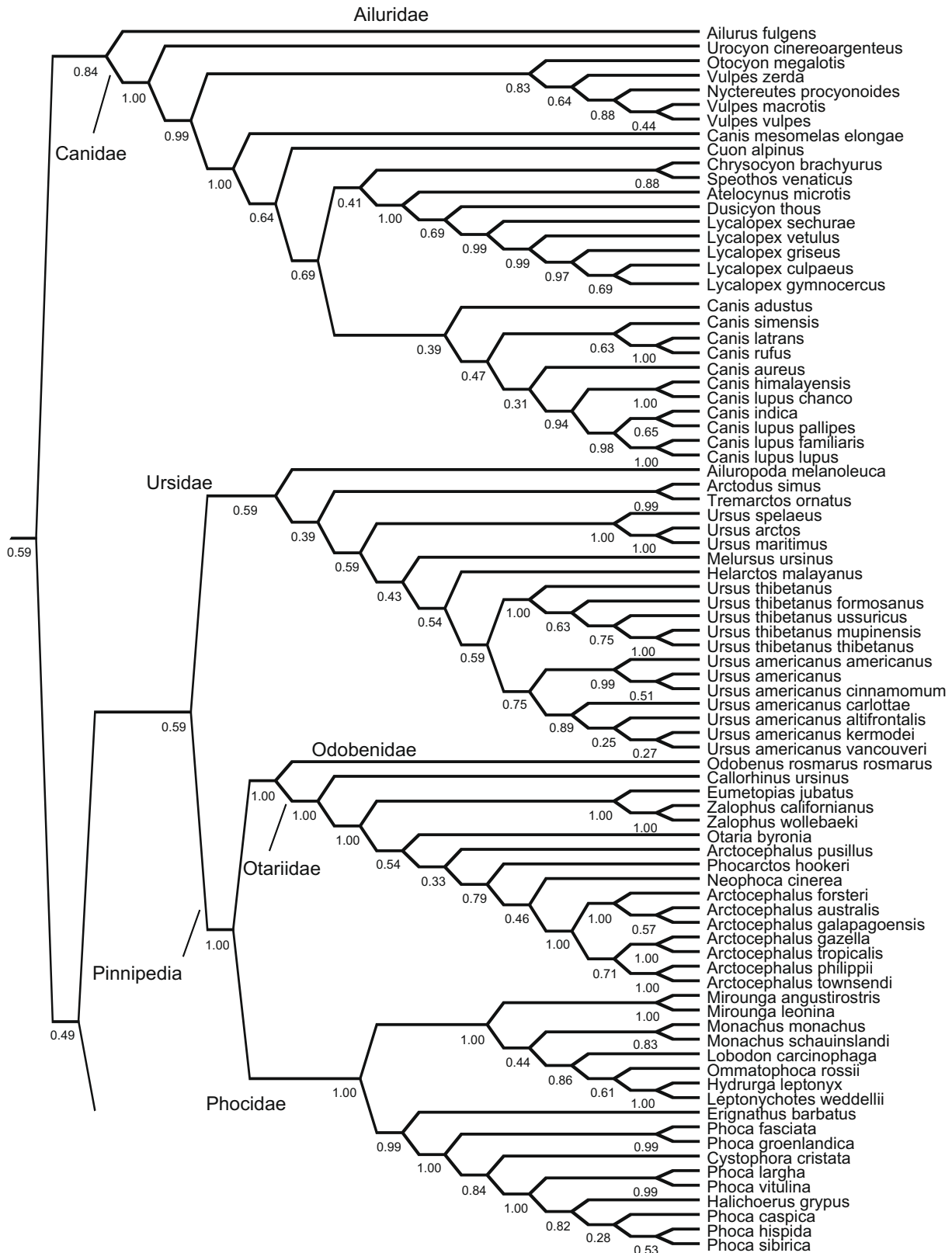


Fig. 6. Details of relationships among caniformian carnivores, see also Fig. 7. Numbers are posterior probability values.

4.2.1. Canidae

Our study places the gray fox (*Urocyon cinereoargenteus*) sister to other extant canids (Fig. 6). Several other studies based on a combination of morphological, behavioral, cytogenetic, and mtDNA

data for 23 species (Zrzavy and Ricankova, 2004), nuclear DNA (Bardeleben et al., 2005), and combined molecular and morphological data (Wayne et al., 1997) support the same relationship. The gray fox thus represents an old lineage that has persisted but not

diversified compared to its sister lineage, despite the ecological success of this species judged by its current abundance.

Like in these prior studies, our findings refute the monophyly of *Canis* with the black-backed jackal (*Canis mesomelas*) and dhole or Asian wild dog (*Canis*, or *Coua alpinus*) sister to the remaining canids. Similar to Wayne et al. (1997) we found support for a clade containing *Cerdocyon* (= *Dusicyon*, crab-eating dog) and *Atelocynus* (short-eared dog) and *Pseudalopex* (foxes, previously *Lycalopex*).

Our findings place the domestic dog sister to the Eurasian wolf (*Canis lupus lupus*), thus agreeing with previous findings that the dog was domesticated from it (e.g., Vila et al., 1997).

4.2.2. Ursidae

Within Ursidae, the giant panda (*Ailuropoda melanoleuca*) is sister to the remaining ursids (Fig. 6). Other recent studies have also suggested that the giant panda branched off prior to the major diversification of Ursidae (Yu et al., 2004; Fulton and Strobeck, 2006; Pages et al., 2008; Krause et al., 2008). The spectacled bear (*Tremarctos ornatus*) and the extinct giant short-faced bear (*Arctodus simus*), who share with the panda conspicuous black patches around the eyes, vegetarian diet, and arboreal habits, then branch off next, as also found by Krause et al. (2008).

Our results refute the monophyly of the genus *Ursus*, as the monotypic sloth bear (*Melursus ursinus*) and sun bear (*Helarctos malayanus*) nest within it. Therefore, we support Krause et al. (2008) in transferring these species to *Ursus* (as *U. ursinus* and *U. malayanus*, respectively). Like Krause et al. (2008) we found strong support for the following relationship: *Ursus spelaeus* (cave bear) sister to *Ursus arctos* (brown bear) + *U. maritimus* (polar bear). In addition, our study concurs with other molecular studies (Krause et al., 2008; Talbot and Shields, 1996a,b) supporting a sister relationship between *U. thibetanus* and *U. americanus*, contrasting the results by Pages et al. (2008) using nuclear genes.

4.2.3. Pinnipedia—Odobenidae, Otariidae, Phocidae

Several studies have supported the monophyly of Pinnipedia, the majority of them based on molecular evidence (e.g., Davis et al., 2004; Arnason et al., 2006, 2007; Sato et al., 2006; Dragoo and Honeycutt, 1997; Higdon et al., 2007). The relationships found in our study within Pinnipedia (Fig. 6) agree with previous studies supporting the monophyly of each family, as well as placing seals (Phocidae) sister to Otarioidea containing eared seals and the walrus (Odobenidae + Otariidae) (e.g., Davis et al., 2004; Arnason et al., 2006, 2007; Higdon et al., 2007).

In concordance with previous molecular studies, the monophyly of the Otariidae subfamilies, initially proposed based on vague morphological data (Repenning et al., 1971; King, 1983), is refuted. *Arctocephalus* (fur seals) is again refuted due to the phylogenetic position of the South African (or Cape) fur seal (*A. pusillus*), which has been referred to as ‘enigmatic’ (Bininda-Emonds et al., 1999; Wynen et al., 2001; Higdon et al., 2007). Wynen et al. (2001) using partial cytb and control region sequences found some support for the relationship between *A. pusillus* and *A. tropicalis*, the subantarctic fur seal. In our study, however, it is placed in a grade of sea lions within which the remainder of *Arctocephalus* are monophyletic.

Our study provides strong support for the placement of *Callorhinus ursinus* (northern fur seal) sister to the rest of otariids (Fig. 6). In agreement with prior studies our results support a sister relationship between *Eumetopias* (Steller sea lion) and *Zalophus* spp. (sea lions) (e.g., Wynen et al., 2001; Higdon et al., 2007). Further, we found a clade containing *Otaria* (South American sea lion), *Phocarctos* (New Zealand sea lion), *Neophoca* (Australian sea lion), and *Arctocephalus* (fur seals) (see also Higdon et al., 2007). The relationships within this second lineage include strong supported southern hemisphere clade containing *A. forsteri* (New Zealand

fur seal), *A. australis* (South American fur seal), and *A. galapagoensis* (Galapagos fur seal), suggesting the colonization of Galapagos from Southern America. The sister relationship of *A. tropicalis* (Subantarctic fur seal) and *A. gazella* (Antarctic fur seal) also represents an expected biogeographical pattern, however, more curious is the sister relationship between *A. philippii* (Juan Fernandez fur seal) and *A. twonsoni* (Guadalupe fur seal) suggesting a long distance dispersal to the Juan Fernandez islands.

4.2.4. Musteloidea—Mephitidae, Procyonidae, Mustelidae

Within Musteloidea our results differ in relationships among major groups from the recent study of Arnason et al. (2007) which found support for the following relationship (*Ailurus*(Mephitidae(Procyonidae), Mustelidae)). Instead we find a sister relationship between Mephitidae and Procyonidae, and that *Potos flavus* is sister to all other musteloideans (Fig. 7). With the exception of the suggested position of *Ailurus*, the musteloidean family relationships that we support here have previously been supported by mitochondrial and nuclear data (Flynn et al., 2005) and supertree analysis (Bininda-Emonds et al., 1999).

Our results strongly place *Potos flavus* (kinkajou) as sister to all musteloideans thus rendering Procyonidae paraphyletic. This is a somewhat surprising result, given that a recent study by Fulton and Strobeck (2007) based on nuclear and mitochondrial DNA and a study by Koepfli et al. (2007, see Fig. 3) based on a combined analysis of 11 gene segments supported the monophyly of Procyonidae. However, in these studies *Potos* was sister to the remaining Procyonidae, and was considered ‘highly autapomorphic’. This is another example of a difference between a taxon rich versus character rich studies (Agnarsson and May-Collado, 2008), and we must consider the placement of *Potos* an open question. Otherwise, the relationships between procyonid species resemble those by Fulton and Strobeck (2007) and Koepfli et al. (2007), where a subclade contains both *Procyon* spp. (raccoons) sister to *Bassariscus* spp. (ringed-tailed) and another subclade consist of *Nasua* spp. (coatis) sister to *Bassaricyon* spp. (lingons).

Although in our study the monophyly of Mustelidae is supported, subfamilies within it are not. Sato et al. (2003, 2004) using nuclear genes also found Mustelinae to be paraphyletic (see also Stone and Cook, 2002). Koepfli and Wayne (1998) similarly suggested paraphyletic Lutrinae. In other aspects our results contrast the cytb study of Koepfli and Wayne (1998), which must be related to a denser taxon sampling in our study. In contrast to our findings, Dragoo and Honeycutt (1997) based on 12S and 16S ribosomal RNA (rRNA) genes, found support for the monophyly of Lutrinae, and Marmi et al. (2004) using cytb and repetitive flanking regions, found support for the monophyly of Melinae, Lutrinae, and Mustelinae.

4.2.5. The phylogenetic position of the red panda (*Ailurus fulgens*)

The phylogenetic position of the red panda has been one of major controversies in the history of Carnivora phylogenetics. Most studies have placed it within Arctoidea, but differed in its exact phylogenetic position (e.g., Delisle and Strobeck, 2005 [mtDNA], Flynn et al., 2005 [nuDNA, mtDNA], Flynn et al., 2000 [morphology and molecular data] Sato et al., 2006 [nuDNA], Fulton and Strobeck, 2006 [nuDNA], Arnason et al., 2007 [complete mitogenomic data]). Most studies placed the red panda in Musteloidea. Delisle and Strobeck (2005) suggested a sister relationship between the red panda and Mephitidae; while Sato et al. (2006) and Fulton and Strobeck (2006) proposed a clade containing the red panda, Procyonidae, and Mustelidae; and Arnason et al. (2007) found support for the position of the red panda as sister to (Mephitidae(Procyonidae, Mustelidae)). In addition, Slattery and O’Brien (1995) suggested (based on very few species) that the red panda diverged early within the lineage of Procyonidae. Our results suggest two alternative

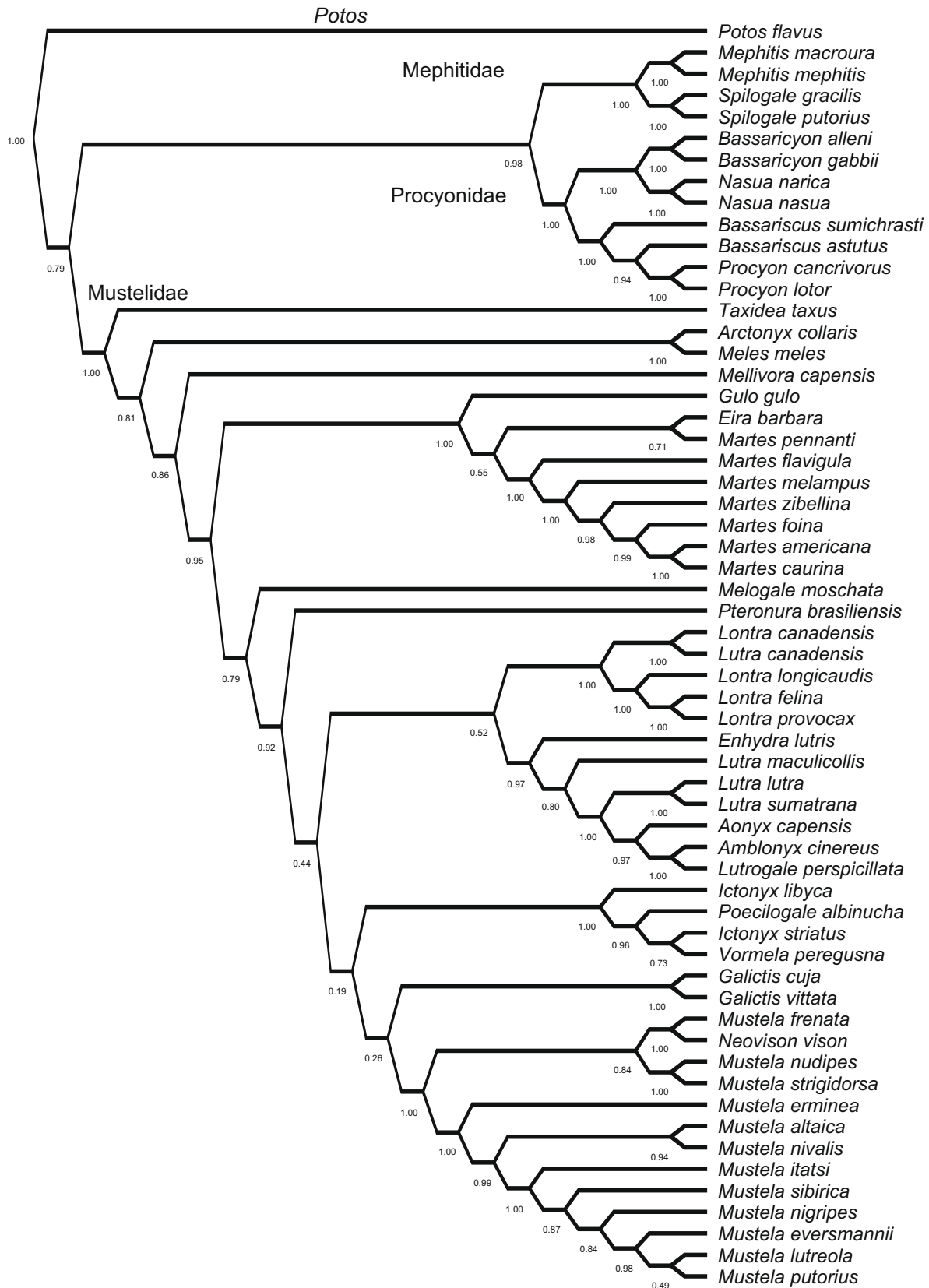


Fig. 7. Details of relationships among caniformian carnivores, see also Fig. 6. Numbers are posterior probability values.

and novel placements, the Bayesian analysis supports a sister relationship between the red panda and Canidae with relatively strong support, which challenges the monophyly of Arctoidea. The likeli-

hood analysis places the red panda sister to all Caniformia minus Canidae. Essentially the difference between the two methods is a matter of root placement within Caniformia, the position of the

red panda in the phylogenetic network is the same in the two analyses. Either finding is surprising given prior work, but underlines the uncertainty surrounding the phylogenetic affinities of this enigmatic animal.

4.3. Relationships within Feliformia

Our results support the monophyly of all families within Feliformia (Figs. 1–5) (Barycka, 2007; Gaubert and Cordeiro-Estrela, 2006). Our Bayesian results support several studies, which suggested the African palm civet *Nandinia binotata* (Nandiniidae) as sister to a clade containing the remaining extant feliformians (Flynn and Nedbal, 1998; Wesley-Hunt and Flynn, 2005; Flynn et al., 2005; Finarelli and Flynn, 2007). Both Bayesian and likelihood here agree that it is not a true civet (Viverridae). In terms of genetic diversity, therefore, this species represents an ancient lineage and thus much unique evolutionary history. Fortunately, it is not currently under threat (IUCN, 2009). In the likelihood analysis, *Nandinia* instead is sister to cats, highlighting that some of the interrelationships among Feliformia families are here poorly supported.

Our results agree with recent molecular phylogenies (mtDNA and nuDNA) that have found support for a sister relationship between Viverridae and the remaining feliformians (e.g., Flynn et al., 2005; Gaubert and Cordeiro-Estrela, 2006). Further, prior studies have also supported the following relationship (Hyaenidae (Eupleridae + Herpestidae)) (e.g., Flynn et al., 2005; Gaubert and Cordeiro-Estrela, 2006; Finarelli and Flynn, 2007). Our results place Prionodontidae (linsangs) as sister to the above clade. However, as discussed above, these interrelationships are poorly supported and quite different in the likelihood analysis (Supplementary Fig. 2).

4.3.1. Viverridae

With the exception of Paradoxurinae, all other three subfamilies (Viverrinae, Genettinae, and Hemigalinae) were monophyletic (Fig. 3), as previously found, e.g., by Gaubert and Cordeiro-Estrela (2006), and Patou et al. (2008). The paraphyly of Paradoxurinae is due to the placement of *Arctogalidia invirgata* sister to Hemigalinae and the rest of Paradoxurinae. This result is consistent with the monotypic subfamily Arctogalidiinae proposed by Pocock (1933). However, Patou et al. (2008) placed *Arctogalidia* sister to the remaining Paradoxurinae (hence a monophyletic Paradoxurinae) based on mtDNA and nuDNA. *Arctogalidia* is morphologically peculiar and its placement requires further scrutiny. Apart from *Arctogalidia*, our results are nearly identical to those of Patou et al. (2008), and very similar to those of Gaubert et al. (2004) using morphological and molecular data, and Gaubert and Begg (2007) using molecular data.

4.3.2. Felidae

The monophyly of Felidae receives strong support (Fig. 4), however, many clades within it are poorly supported, and differ among the analyses. The low support seems in large part to be due to missing data—the high number of felids with short sequences, average nodal support within Felidae is generally lower in the full dataset than in the pruned dataset. Given the low support for many clades, we focus our discussion on clades that are better supported and thus more likely to withstand the addition of data.

Our results differ from most previously proposed felid phylogenies, but this is not surprising as prior studies also differed greatly among themselves. Similar to our study, prior studies have some shortcomings. These include low taxon sampling (Bininda-Emonds et al., 2001; Yu and Zhang, 2005; Christiansen, 2008), poor character to taxon ratio (Christiansen, 2008), poor resolution (Yu and Zhang, 2005), or the derivation of the phylogeny from a single, rel-

atively narrow, data source, e.g., animal chemical signals (Bininda-Emonds et al., 2001) or almost exclusively osteological characters (Christiansen, 2008). There is thus little consensus regarding Felidae phylogenetics and a need for more comprehensive studies. The main strength of our study is a threefold increase in taxon sample compared to the largest prior study (Yu and Zhang, 2005), and a much denser outgroup sampling than prior studies (e.g., Christiansen, 2008). We highlight this family here to draw attention to the lack of consensus regarding the phylogenetic relationships within this important and high-profile group of mammals. Gathering more phylogenetic data from a broad taxonomic sample of felids is thus an urgent priority. In the short term, gathering full cytb sequences from cat species can provide the most rapid means to advance understanding of Felidae phylogenetics.

The “big cat clade”, containing *Panthera* and *Neofelis* species, is well supported (Fig. 4). There is good support for monophyly of *Oncifelis*, *Neofelis*, and *Panthera*, relatively weak support for *Prionailurus* and *Felis*, but the genera *Lynx* and *Leopardus* are paraphyletic in our tree. The genera for which monophyly cannot be tested due to monotypy/taxon sample, are *Homotherium*, *Herpailurus*, *Catopuma*, *Pardofelis*, *Acionyx*, *Miracinonyx*, *Puma*, *Lynchailurus*, *Ictailurus*, and *Otocolobus*. However, the short terminal branches and 100% support for the clade *Catopuma* + *Pardofelis* suggest these are synonymous, and thus support the monophyly of *Pardofelis* s.l. Our results dispute the sister group relationship of the jaguarondi (*Herpailurus yagouarundi*) and the puma (*Puma concolor*) (Masuda et al., 1996; Mattern and McLennan, 2000; Johnson et al., 2006), although the exact placement of the jaguarondi remains ambiguous.

Some prior studies have found support for the division of the cats into sister clades of relatively big cats and small bodied cats (Bininda-Emonds et al., 2001). However, the phylogenies of Yu and Zhang (2005) and Johnson et al. (2006), refuted this, as do our findings. The relatively big cats form two distantly related clades, *Neofelis* + *Panthera* and the cheetah (*Acionyx jubatus*), the puma (*Puma concolor*) and the extinct American cheetah (*Miracinonyx trumani*), although the latter three form a grade rather than a clade in the likelihood tree. Nevertheless, such results strongly imply independent evolution towards big size in cats (contra Bininda-Emonds et al., 2001).

The genus *Panthera* includes the four roaring cats (tiger, lion, leopard, and the jaguar, Peters and Hast, 1994; Weissengruber et al., 2002), but also the non-roaring snow leopard (*Panthera uncia* = *Uncia uncia*). All our analyses agree that the latter groups with relatively distal *Panthera* species, suggesting *Uncia* is a junior synonym of *Panthera* (as in Johnson et al., 2006). Other studies place the snow leopard as sister to other species of *Panthera* (Johnson and O'Brien, 1997; Mattern and McLennan, 2000; Christiansen, 2008), implying the single origin of roaring within *Panthera*. Our findings, in contrast, best explain the inability of the snow leopard to roar as secondary loss. The tiger subspecies (*P. tigris*) form a group that is sister to all other *Panthera* species, these in turn separating the lion (*P. leo*) from the clade including the leopard (*P. pardus*), the snow leopard (*Panthera uncia*), and the jaguar (*P. onca*). While these findings are generally well supported, they are incongruent with previously proposed topologies within *Panthera* (Mattern and McLennan, 2000; Bininda-Emonds et al., 2001; Johnson et al., 2006; Christiansen, 2008). We have previously detected such incongruence between taxon sparse versus character sparse phylogenies (Agnarsson and May-Collado, 2008; May-Collado and Agnarsson, 2006): further studies including both many taxa and many characters are needed to resolve them.

Our results group a Neotropical big cat, the jaguar, with the enigmatic cat form the Central Asian mountain ranges, the snow leopard (Bayesian analysis) or the leopard (likelihood). This clade is nested within an Old World big cat group making it difficult to

interpret biogeographically. The modern cat radiation is much too recent (<11 mio years ago; Johnson et al., 2006) for vicariance to have played a major role (Mattern and McLennan, 2000). Our findings thus suggest a long-range dispersal of the jaguar ancestor, during glaciations, to the Americas. A similar scenario has been suggested for lions, for example, which expanded their range from Africa to include Europe and the Americas during the Pleistocene (Yamaguchi et al., 2004).

All analyses recovered two distinct clades within the Old World clade *Felis*. One groups the fairly heavy bodied jungle cat (*Felis chaus*) with the small bodied black-footed cat (*F. nigripes*) and the other groups the remaining *Felis* species, all sometimes considered to be subspecies of the Eurasian wildcat, *F. silvestris*. The analysis of Johnson et al. (2006), based on mitochondrial DNA data, placed the domestic cat as sister to the European wildcat (*F. silvestris silvestris*). However, a recent study by Driscoll et al. (2007) tested the origin of cat domestication by genotyping 979 individuals belonging to all *F. silvestris* subspecies from the entire range for 36 short tandem repeats (STR) of DNA and by analyzing two mitochondrial DNA genes. They concluded that cat domestication from as few as five founders took place in the Near East more than 9000 years ago, which dates further back than the archeological evidence for cat domestication from ancient Egypt 5700 years ago (Linseele et al., 2007). The neighbor joining analysis with mitochondrial data of Driscoll et al. (2007) grouped the domestic cat with both *F. s. lybica* and *F. s. ornata*, but their phylogenetic analysis grouped the domestic cat (European and Asian lineages being monophyletic) unequivocally with *F. s. lybica* from the Near East.

Our Bayesian results agree with the findings of Driscoll et al. (2007), in closely grouping the two subspecies *F. s. lybica* and *F. s. ornata* with the domestic cat. However, our results weakly place the domestic cat as sister to the Asiatic wildcat (*F. silvestris ornata*), and the likelihood result placed such clade as sister to the remaining *Felis*. Based both on Driscoll et al. and our study there seems to remain a possibility that the domestic cat was bred from both *F. s. lybica* and *F. s. ornata*, or perhaps only from the latter.

The clade *Neofelis* + *Panthera* groups the biggest cats (*Panthera*) with two medium sized Asian species, the clouded leopard (*Neofelis nebulosa*) and the Bornean clouded leopard (*Neofelis diardi*). This supports Christiansen's (2006) claims of convergent evolution in "saber-tooth" characteristics in the clouded leopard with those in the extinct saber-toothed cats, here represented by *Homotherium*. The sister relationship of the puma and the extinct American cheetah is well supported, suggesting diversification within America. These, in turn, group with the African cheetah, the fastest land animal and an unusual cat considering its diminished claw retraction abilities (Russell and Bryant, 2001). However, support for this relationship is Bayesian only and is too weak to allow preliminary speculations on the running and climbing abilities of the American cheetah.

4.3.3. Prionodontidae, Hyaenidae, Eupleridae, and Herpestidae

The monophyly of Prionodontidae, Hyaenidae, and Herpestidae are all strongly supported here (Fig. 3), while Eupleridae is weakly supported. The interrelationships of species within Hyaenidae differ slightly from those suggested by Koepfli et al. (2006) in strong

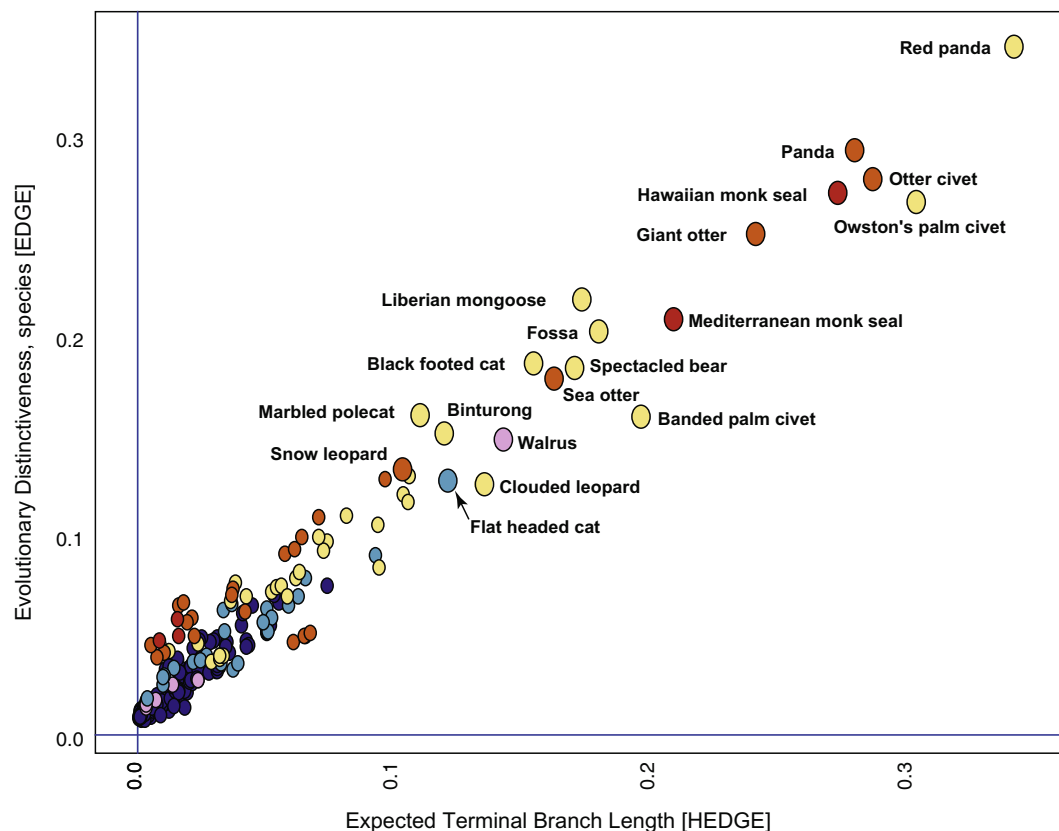


Fig. 8. A scattergram of two conservation priority metrics, EDGE and HEDGE, under the 'pessimistic' transformation of IUCN categories to extinction risk, see text. Species ranking high in both analyses are highlighted (for details, see Supplementary Table 1). Colors of dots refer to IUCN conservation status, with dark blue reflecting least concern, light blue indicating near threatened, yellow indicating vulnerable, orange indicating endangered, and dark red critically endangered, respectively. Pink indicate 'data deficient' species (see text). It is notable that a number of endangered and critically endangered species rank lower than many species that are not currently seriously threatened. Species such as the walrus (currently listed as data deficient, but recently as least concern) and flat headed cat (near threatened) rank high, reflecting their evolutionary distinctiveness, while some endangered species have closely genetically similar, less threatened, relatives. Hence, losing these endangered species would lose relatively little unique evolutionary diversity. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

support for a sister species relationship between the aardwolf (*Proteles cristatus*) and the spotted hyena (*Crocuta crocuta*), instead of grouping the hyenas together. This implies that the insectivorous habits of the aardwolf evolved within this clade of otherwise hunters/scavengers. Within Eupleridae the subfamily Galidiinae (*Galidia*, *Galidictis*, *Mungotictis*, and *Salanoia*) was supported, while Euplerinae (*Cryptoprocta* and *Fossa*) was not. However, the exact placement of *Fossa* is very weakly supported. Our results are similar to those of Gaubert and Cordeiro-Estrela (2006) based on molecular data, but contrast considerable to morphological based phylogenies (see Gaubert et al., 2005).

Within mongooses (Herpestidae), our results are in general similar to Veron et al. (2004). Notably, the genus *Herpestes* is polyphyletic, suggesting serious taxonomic problems within the family as also found by Veron et al. (2004) based on complete cytb sequences and eco-ethological characters.

4.4. Conservation priorities

As one potential application of phylogenetic results such as ours, we conclude by providing a preliminary phylogenetic assessment of conservation priorities within Carnivora (Fig. 8). The EDGE (Isaac et al., 2007) and HEDGE (Steel et al., 2007) metrics consider both evolutionary distinctiveness (i.e., how much unique evolutionary history the species represents) as well as extinction risk, to assess how conservation efforts might profitably be prioritized (Vane-Wright et al., 1991). What to protect? Clearly, many other factors play a role when conservation priorities are assessed, including ecological role of species, economic value, charisma, etc. Furthermore, how one estimates extinction risk of species strongly impacts EDGE and HEDGE analyses (Mooers et al., 2008). Thus we do not intend this preliminary analysis as a guideline to, e.g., how to allocate funding to conservation effort in Carnivora—a more detailed analysis will be presented elsewhere (May-Collado and Agnarsson, in preparation). However, it does provide information beyond mere extinction risk of species, to what species contain much unique evolutionary history, and thus should be considered as important for conservation of evolutionary diversity. Based on this, our analysis underlines the importance of many ongoing conservation efforts for species such as monk seals, giant and red panda, snow leopard, and giant and sea otters, but also highlights species which have received relatively less conservation attention such as the Liberian mongoose, the binturong, and the highly evolutionary distinct walrus.

5. Conclusions

We provide a novel species based phylogeny of Carnivora containing about 82% of the known taxonomic diversity of the dogs, cats, and their kin. The primary purpose of the study is to provide a tool for comparative, species-level, comparative studies of carnivores that supplements existing supertrees. As our results largely agree with the best supported clades that prior studies agree on (benchmark clades), the hypothesis we propose here should, overall, be a useful tool. As we have previously found for Cetartiodactyla, cytb is an extraordinary phylogenetic marker when taxa are densely sampled, and thus a good candidate for rapid improvement in phylogenetic knowledge of large clades. In terms of the basic subdivision of Carnivora into cat-like (Feliformia) and dog-like (Caniformia) animals, and the placement of carnivoran species in families, phylogenetic understanding of carnivores seems strong. However, our study, as have others before, point to several problematic issues with taxonomy at lower levels, and some unresolved issues in terms of placement of some families. In general, our study highlights the need for additional sampling of full-length cytb se-

quences as a rapid means of estimating phylogenetic relationships, and the collection of other types of data where a broad taxon sampling is better emphasized than in studies hitherto. Our analyses highlight species that may deserve special conservation attention if we are to maximally preserve evolutionary diversity on our planet.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ymp.2009.10.033.

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