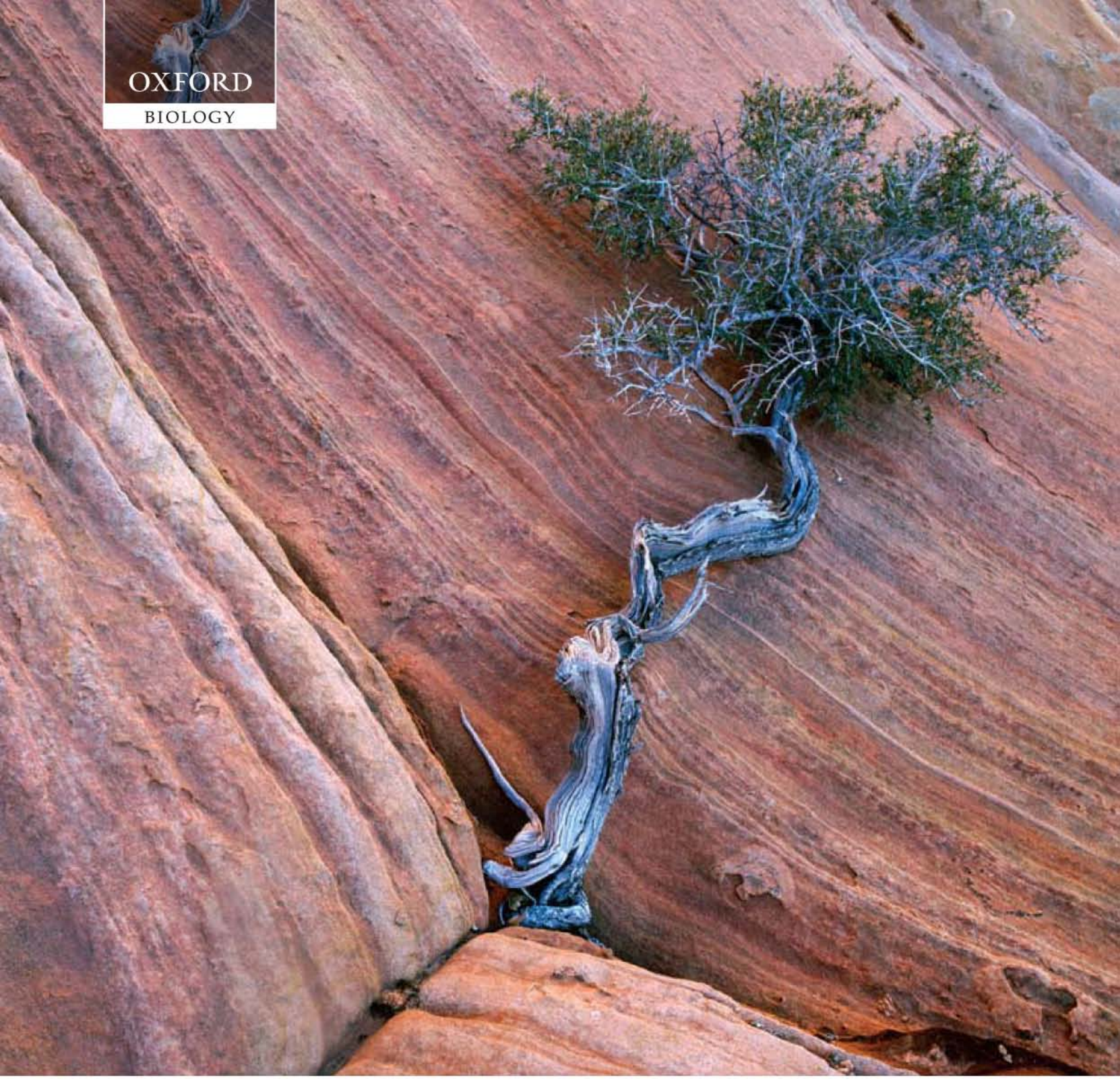

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Carnivores (Carnivora)

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Abstract

Living members of the mammalian Order Carnivora have been traditionally placed in 11 families making up two suborders: Feliformia and Caniformia. Recent analyses based on morphological and molecular data have identified additional groups of species that warrant family-level recognition, leading to major changes in the current understanding of carnivoran evolutionary history and taxonomy. There are presently 16 recognized families, whose relationships are now well understood. The carnivoran timetree indicates that Feliformia and Caniformia diverged from each other ~55 million years ago (Ma). Within each suborder, suprafamilial nodes span a broad range of divergence times, from 53 to 22 Ma.

The Order Carnivora contains a diverse set of mammals, including well-known species such cats, dogs, lions, bears, and seals, as well as enigmatic animals such as the stink badgers (*Mydaus* spp.), the African Palm Civet (*Nandinia binotata*), and the Fossa (*Cryptoprocta ferox*). There are currently 286 recognized species of living carnivorans (e.g., Fig. 1), which vary widely in morphology, ecology, physiology, and behavior (*1, 2*). Size range among carnivoran species is broader than in any other mammalian order, with body weight varying 1000 times among its representatives. The Order Carnivora has a relatively rich paleontological record. The earliest fossils, dating from the Paleocene (66–56 Ma), are usually placed in the extinct families Viverravidae and Miacidae (*3*), both of which likely comprise early branching lineages relative to the living taxa (*4*). The carnivoran fossil record from the Paleocene to the Oligocene (34–23 Ma) is confined to Eurasia and North America (*4*), supporting the view that this mammalian order has had its origin in Laurasia. Only in the Miocene (23–5 Ma) do carnivoran families appear in the fossil records of Africa and South America, indicating an initial period of intercontinental dispersal in this group. Here we review the current understanding of the phylogenetic relationships and divergence times among carnivoran families, focusing exclusively on living lineages, and emphasizing results from recent studies.

Living members of the Order Carnivora are grouped into two monophyletic suborders: Feliformia and Caniformia. The former traditionally included Families Viverridae (e.g., civets and genets), Herpestidae (mongooses), Hyaenidae (hyenas), and Felidae (cats), while the latter comprised the Families Canidae (dogs, wolves, and foxes), Mustelidae (e.g., otters, weasels, and badgers), Ursidae (bears), Procyonidae (e.g., raccoons and coatis), Otariidae (sea lions and fur seals), Phocidae (true seals), and Odobenidae (Walrus). Otariidae, Phocidae, and Odobenidae are highly adapted for marine life and have been historically grouped in a taxon called Pinnipedia. The monophyly and phylogenetic placement of pinnipeds have been contentious for many years (*2, 5, 6*), but this issue seems to be mostly settled now (*7–10*). It is now clear that Pinnipedia is monophyletic and that

Fig. 1 An African Wild Dog (*Lycaon pictus*), representing the Family Canidae (Caniformia), from Kruger National Park, South Africa. Credit: E. Eizirik.

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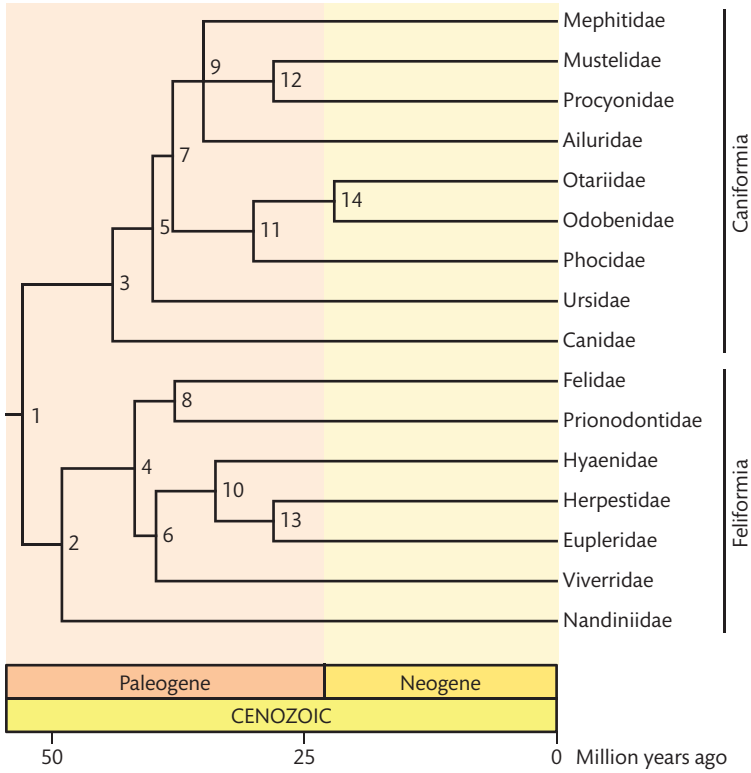

Fig. 2 A timetree of carnivores (Carnivora). Divergence times are shown in Table 1.

it is contained in Arctoidea (pinnipeds + Ursidae + Mustelidae + Procyonidae + Red Panda + skunks (see later)), which is nested within the carnivoran Suborder Caniformia.

In addition to the argument over the relationships of Pinnipedia, several other aspects of the carnivoran tree have been contentious over the last few decades, leading to the production of a large body of literature on the phylogeny of this mammalian order (e.g., *4–30*). Most of the effort has been traditionally focused on the Caniformia, and particularly on the positions of the Giant Panda (*Ailuropoda melanoleuca*), Red Panda (*Ailurus fulgens*), and skunks (originally placed in the Mephitinae within Mustelidae, but now recognized as comprising a separate family, Mephitidae). On the feliform side, the monophyly of the Family Viverridae has been challenged multiple times, starting with the proposition that the African Palm Civet (*N. binotata*) was actually not a member of this family, but rather the only living representative of the most basal extant lineage of the Feliformia (e.g., *4, 24, 25*). Another feliform whose phylogenetic affinities have historically been enigmatic is the Fossa (*C. ferox*), a Malagasy carnivoran with unique morphological and behavioral characteristics often placed in Viverridae, Herpestidae, or in its own monotypic family (*1, 2, 26*). The last few years have seen a surge in studies on these and other topics of the carnivoran phylogeny (e.g., *7–10, 18–23*) most of which used concatenations of multiple nuclear and/or mitochondrial genes. This has led to a consistent resolution of most suprafamilial nodes (Fig. 2), settling many of the disputes briefly outlined earlier. The Giant Panda was established as the most basal extant ursid, and the Red Panda is now placed in its own monotypic family (Ailuridae), nested in Arctoidea. Skunks and stink badgers (*Mydaus* spp.) are closely related, and together constitute the Family Mephitidae, which is not immediately connected to the Mustelidae (*14, 15, 28*). Another recent finding is that Mustelidae and Procyonidae are each other's closest relatives, an observation which is supported by several studies (e.g., *8, 15, 24*). There is a core group in Arctoidea containing Mephitidae, Ailuridae, and Mustelidae + Procyonidae, whose internal structure has still not been confidently resolved (Fig. 2). Pinnipedia is now seen as the closest relative of this core clade, with Ursidae being

Table 1. Divergence times (Ma) and their confidence/credibility intervals (CI) among carnivores (Carnivora).

Timetree		Estimates													
Node	Time	Ref. (*19*)		Ref. (*22*)		Ref. (*23*)		Ref. (*30*)		Ref. (*31*)		Ref. (*32*)		Ref. (*33*)	
		Time	CI	Time	CI	Time	CI	Time	CI	Time	CI	Time	CI	Time	CI
1	52.9	–	–	–	–	–	–	–	–	55.0	60–51	57.5	62–52	46.2	57–35
2	49.0	–	–	54.6	–	–	–	43.3	54–33	–	–	–	–	–	–
3	44.0	–	–	–	–	44	–	–	–	–	–	–	–	–	–
4	41.8	–	–	47.0	–	–	–	36.5	47–29	–	–	–	–	–	–
5	40.0	–	–	–	–	40	–	–	–	–	–	–	–	–	–
6	39.7	–	–	44.2	–	–	–	35.2	45–28	–	–	–	–	–	–
7	38.0	–	–	–	–	38	–	–	–	–	–	–	–	–	–
8	37.8	33.3	35–32	42.3	–	–	–	–	–	–	–	–	–	–	–
9	35.0	–	–	–	–	35	–	–	–	–	–	–	–	–	–
10	33.8	–	–	38.3	–	–	–	29.2	38–23	–	–	–	–	–	–
11	30.0	–	–	–	–	30	–	–	–	–	–	–	–	–	–
12	28.0	–	–	–	–	28	–	–	–	–	–	–	–	–	–
13	28.0	–	–	31.6	–	–	–	24.4	32–18	–	–	–	–	–	–
14	22.0	–	–	–	–	22	–	–	–	–	–	–	–	–	–

Note: Node times in the timetree represent the mean of time estimates from different studies.

the most basal lineage in Arctoidea. Canidae is indeed the most basal family in the Caniformia, supporting the traditional view that it is the only extant lineage of the Superfamily Cynoidea.

Among feliforms, recent studies have led to major changes in the prevailing views on phylogenetic structure and evolutionary history. Two separate studies published in 2003 have shown further evidence of viverrid paraphyly, and identified novel lineages that are now recognized as valid families (*19, 20*). Asian linsangs (*Prionodon* spp.), traditionally part of the Viverridae, have been shown to be the closest relative of the Felidae (*19*), and are now placed in their own family, Prionodontidae (*21*). Another remarkable finding was that all Malagasy carnivores (including the Fossa), traditionally placed in the Viverridae or Herpestidae, comprise a separate, endemic monophyletic lineage (*20*), which is now recognized as Family Eupleridae. In addition, all recent studies that included *Nandinia* confirmed that this taxon is indeed the most basal feliform, and now constitutes its own family, Nandiniidae (*1*). As a whole, these recent studies have challenged not only the monophyly of traditionally recognized Viverridae, but also the monophyly of Herpestidae, restructuring the feliform phylogeny to a large degree. Most suprafamilial nodes in this suborder have now been consistently resolved by independent studies (Fig. 2). Felidae and Prionodontidae are each other's closest relatives, as are Eupleridae and Herpestidae. Hyaenidae is the closest relative of the Eupleridae + Herpestidae clade. The relative position of Viverridae (now restricted to a monophyletic core group) has not been confidently established with high support, though most studies indicate that it is more closely related to the Hyaenidae + Eupleridae + Herpestidae clade (Fig. 2).

Although many studies have addressed carnivoran relationships, few have assessed the age of the inferred clades using molecular data. The results reviewed here are drawn mostly from four recent studies, which have separately addressed each of the two carnivoran suborders (*19, 22, 23, 30*). The basal divergence between Feliformia and Caniformia seems to have occurred between the Paleocene and the middle Eocene (49–40 Ma), with the dates used here being derived from large studies involving all placental mammal clades (*31, 32*) or multiple vertebrate groups (*33*). Within Feliformia, the divergence between Nandiniidae and the other lineages was estimated by one study to be ~43 Ma (*30*), and by another to be ~55 Ma (*22*); the latter may be an overestimate given the branch length observed in multiple studies between the feliform–caniform split and this basal feliform node. The dates obtained in this study (*22*) are consistently older than equivalent divergence times

obtained by other papers (*19, 30*), in some cases lying outside of the estimated confidence intervals (Table 1). Further investigations are required to better understand this discrepancy and generate a more reliable and consensual view on feliform divergence times.

Within Caniformia, the only published study describing molecular estimates of divergence times places the basal split between Canidae and Arctoidea at 44 Ma, consistent with the fossil record for this group (*23*). Overall, suprafamilial divergences in the Carnivora seem to occur almost exclusively in the Paleogene, mostly concentrating in the Eocene and early Oligocene (53–34 Ma). Additional divergence dating studies are needed for this group, especially using the same data set for Feliformia and Caniformia, and employing multiple fossil calibrations. The reliability of fossil calibrations may be an issue (e.g., addressed in *22*), since the exact phylogenetic placement of some extinct carnivorans may be uncertain or incorrect, potentially leading to biased dating results. It is therefore important to evaluate multiple calibrations simultaneously, and to assess their consistency. The next few years will likely see the consolidation of the carnivoran phylogeny at family, genus, and possibly species level, with accompanying progress on the reliability and precision in divergence time estimates for all included nodes. This will allow a much better understanding of the evolutionary history of extant lineages, and an improved framework upon which to investigate phylogenetic, biogeographic, morphological, and ecological aspects of extinct carnivoran groups.

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