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THE CENTER OF ORIGIN OF TERRESTRIAL MAMMALIAN CARNIVORES AND THEIR FAST BODY MASS EVOLUTION ASSOCIATED TO LONG-DISTANCE DISPERSAL

Tesis presentada a la Facultad de Ciencias Naturales y Oceanográficas de la Universidad de Concepción para optar al grado de Doctor en Sistemática y Biodiversidad

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Tabla de Contenido

GENERAL ABSTRACT

Fundamental tasks to understand the spatial distribution of biodiversity are to estimate where and when species originated, and how did they disperse over space and throughout new environments, in addition to explaining the evolutionary responses associated with this geographical movement. However, these estimations have been difficult to obtain because knowing the centers of origin and tracing the historical paths of species at macro scales has always been a hard challenge. Here, using a novel phylogenetic approach that considers the nature processes in a more accurate way at macro scales and the geographical information of both extinct and extant diversity, we (1) estimated the center of origin of all ancestral species of terrestrial mammalian carnivores and their dispersal routes, and (2) evaluate whether the dispersal ability or trans-continental dispersals implies a fast evolution in body size due the selective pressures of the environment. This doctoral thesis postulates that North America is an important center of origin of early lineages, as the complete clade of mammalian carnivores, the Oxyaenidae† and Carnivoramorpha groups, except for Hyaenodonta† whose origin was in Europe. North America is the place of origin for the order Carnivora and the subfamilies Feliformia and Caniformia. 350 of the 2632 (13.3%) geographical distances estimated correspond to trans-continental dispersal events during the biogeographical history of terrestrial mammalian carnivores. Also, the long-distance dispersal (LDD) explains the fast evolutionary change found in several independent and mainly recent lineages of terrestrial mammalian carnivores and thus their highly discrepant body sizes. Therefore,

this thesis means a significant contribution to understanding the origin and distribution of terrestrial mammalian carnivores, achieving the biogeographical relevance of postulating a new center of origin for the complete group and the current order Carnivora, estimating for the first time the geographical distance traveled for all lineages and explaining how this biogeographical process explain the phenotypical evolution of the group.

GENERAL INTRODUCTION

Historical biogeography

Historical biogeography is the scientific approach that studies the patterns and causes of the distribution of lineages in space, trying to understand the long-standing relationships between biodiversity and geography. Given the spatiotemporal amplitude of the questions that are tried to be answered from this approach, an understanding, at least associative, of the abiotic domain and its consequence in the biotic domain at deep geological scales is required, for example, tectonic events and climate change as causes of vicariance, dispersal, and/or diversification of lineages (Nelson & Platnick 1980; Morrone & Crisci 1995; Wiens & Donogue 2004; Badgley et al. 2017). In this sense, several authors have been emphatic in proposing the integration of the identity of the biotic component as a result of the interaction of biodiversity with geography and its heterogeneous variation on Earth (for example, Grinell 1924; Benton 2009). In the (deep and recent) past, the ecological and/or evolutionary opportunities provided by geographic space have allowed the occurrence of different paleo-biogeographic events that have spatially shaped the identity and distribution of biodiversity (Pianka 1966; Rohde 1992; Nichols et al. 1998; Myers et al. 2000).

Geography, particularly physical geography (Strahler & Strahler 1989; Christopherson & Byrne 2009), can be broken down into elements such as topography and climate, which have been postulated as the main abiotic "drivers" of biodiversity on large spatiotemporal scales (Hawkins et al. 2003; Coblentz & Riitters 2004; Rahbek et al.

2007; Badgley 2010; Badgley et al. 2017). The topography, that is, the arrangement of the natural and man-made physical characteristics of an area (for example, relief, slope, the curvature of the slope, the length of the slope), can be considered as the route or path where biodiversity has availability for movement and displacement (von Humboldt 1808; Hawkins et al. 2003). Regarding topographic spatiality, a disproportionate portion of biodiversity (using “species richness” as a proxy here) occurs within topographically complex regions, such as large mountain ranges and deeply dissected plateaus (e.g., Körner 2004; Antonelli 2015; Merckx et al. 2015; Perrigo et al. 2020; Vallejos-Garrido et al. 2023). Thus, the increasing topographic complexity can create new habitats, widen environmental gradients, establish dispersal barriers, and isolate populations (vicariance), potentially contributing to adaptation to new environmental conditions and the diversification of at least terrestrial species. About topographic temporality, the changes in species richness after tectonic episodes that alter the gradients or geographic barriers allow the dispersion and/or isolation of populations (Kohn & Fremd 2008; Badgley 2010). Although the effect of geography on the generation of spatial patterns and evolution of biodiversity (at least terrestrial) is well documented, there are still certain methodological limitations in including the natural dynamics of geographical processes. For instance, the main current methodological approaches to evaluate the biogeographic patterns and processes assume that species "jump" between the discrete geographical areas previously defined (generally, continents or bioregions) without considering the three-dimensionality of the geographic space and the continental drift (Ronquist 1997; Ree et al. 2005; Ree & Smith 2008; Matzke 2013; O’Donovan et al. 2018).

However, the abiotic component is only a part of the biogeography approach, which requires the intrinsic characteristic of the lineages to be understood, such as the ability of organisms to move and disperse over geography or the evolution of specific traits involved in the geographical movement. In this sense, the "dispersal ability", that is, how much geographical distance organisms can travel; whether they are individuals, populations, or metapopulations; is a fundamental attribute of life history, as it ecologically influences demography and colonization, and from an evolutionary perspective on the flow of genes, rates of local adaptation, speciation, and extinction (Lester et al. 2007). For example, within a metapopulation dynamic, populations can move away from each other depending on the differential "travelled distances" and their "settlement" depends both on the abiotic characteristics of the new geographic space used [niche fundamental Grinell (1917)] as well as the possible relationships and ecological interactions that can be found in this new area [niche made Elton (1927)]. Thus, individuals, populations, and metapopulations must move short or long distances between spatially suitable patches through a matrix of unsuitable habitats to obtain nutritional resources and mating opportunities. Consequently, lineages record different geographic distances finding new places to live where they can potentially adapt and diversify under new environmental conditions (Schooley & Wiens 2003). Thus, the evolution of the lineages during their geographical movement (dispersal) could go hand with the farther there can move from their centre of origin (Hillman et al. 2014; Stevens et al. 2014).

According to the macroevolutionary and biogeographical context of this research, I will define "dispersal" as the geographic movement of "species" from its center of origin, under the understanding that a "species" corresponds to the independent evolution of a Metapopulational lineage (De Queiroz 2007). So, studies at large scales have emphatically argued that long-distance dispersal capacity should be considered a relevant process in the evolution and speciation of lineages (Givnish & Renner 2004; Renner 2004; Cook & Crisp 2005; Halas et al. 2005; De Queiroz 2005; Gillespie et al. 2012) and that differential dispersal abilities can or do not colonize geographically isolated sites (e.g., Peake 1981; Vences et al. 2004; Whittaker & Fernández-Palacios 2007) despite that several authors consider long-distance dispersal to be inherently stochastic (Croizat et al. 1974; Nelson & Platnick 1980; Craw 1982; Humphries 2001; McCarthy 2003). Gillespie et al. (2012) argue that it is necessary the understanding the different modes of long-distance dispersal and the adaptations (and exaptations) associated with this dispersal in the context of geological, paleontological, evolutionary, and ecological data can lead to reconstructions of the origin, frequency of arrival and establishment location of dispersed organisms, as well as subsequent patterns of endemism and diversification. However, like the methodological limitations presented to understand abiotic dynamics, understanding the intrinsic characteristics of lineages is constantly in a methodological update. For example, studying the evolution and distribution of biodiversity at deep times requires using of extinct and extant diversity and their phylogenetical relation in a model that allows the free estimation of ancestral locations and displacement considering the continuous nature of the geographical data.

The mammalian carnivores: The presentation

First, it is necessary to distinguish between mammalian carnivores *sensu lato* and mammalian carnivores *sensu stricto*. The first refers to a non-monophyletic group of mammals that have a carnivorous diet or trophic strategy. That is, they eat predominantly animal foods. Almost all orders of mammals include carnivorous species because this diet has evolved multiple times within different clades of mammals, resulting in repeated convergent morphological adaptations (De Muizon & LangeBadré 1997). The oldest evidence for carnivory in mammals is known from the Early Cretaceous eutriconodontan *Repenomamus* (Hunt et al. 2005). This diet also commonly occurs in other animal lineages, such as reptiles, fish, birds, and even invertebrates. On the other hand, here we refer to mammalian carnivores *sensu stricto* as a monophyletic group of placental mammals made up of the current order Carnivora and their extinct and diverse relatives (Viverravidae†, Hyaenodonta† and Oxyaenidae† clades). The order Carnivora comprises 286 known current species (some representatives in Figure 1), arranged into twenty families, which are grouped into two suborders. The suborder Feliformia includes the families Felidae, Prionodontidae, Hyaenidae, Nandiniidae, Viverridae, Herpestidae, Eupleridae, and the extinct †Nimravidae and †Barbourofelidae; The suborder Caniformia includes the families Canidae, Ursidae, Mephitidae, Mustelidae, Ailuridae, Procyonidae, Phocidae, Otariidae, Odobenidae, and the extinct †Amphicyonidae, and †Desmatophocidae (Hunt 1996; Morlo et al. 2004; Flynn et al. 2010; Eizirik et al. 2010; Nyakatura & Bininda-Emonds 2012).

Figure 1. Some representatives of the order Carnivora. Left, from top to bottom: *Procyon lotor* (Procyonidae), *Otaria flavescens* (Otariidae), *Lycalopex culpaeus* (Canidae); right, from top to bottom: *Nasua narica* (Procyonidae); *Conepatus chinga* (Mephitidae); *Leopardus guigna* (Felidae). All photographs by Paulo Vallejos-Garrido.

The classical phylogenetic proposals show that the order Carnivora + the basal family †Miacidae form a clade called "Carnivoraformes". Numerous authors have remarked on the paraphyly of “miacids” and advocated for abandoning the term (e.g., Spaulding et al.

2010; Spaulding & Flynn 2012). Flynn et al. (2010) erected the group Carnivoraformes to include Carnivora + the “Miacidae” family, and subsequent workers have referred to “miacids” as “basal carnivoraforms” (Solé et al. 2014, Solé et al. 2016). Here we follow this convention. "Carnivoraformes" + the monophyletic family †Viverravidae form a clade called "Carnivoramorpha". The basal carnivoraforms differ from the Viverravidae in the presence of m3 and M3 (Flynn & Wesley-Hunt 2005). Carnivoramorpha was traditionally considered to be the sister clade to † “Creodonta” in the larger clade Ferae, being Creodonta an extinct order that includes the †Hyaenodontidae and †Oxyaenidae families (Gunnell & Gingerich 1991; McKenna & Bell 1997; Gunnell 1998; Wesley-Hunt & Flynn 2005; Flynn et al. 2010; Spaulding & Flynn 2012; O'Leary et al. 2013; Halliday et al. 2017; Prevosti & Forasiepi 2018). Some recent works support the view that “Creodonta” itself is unlikely to be a natural group based on the paucity of well-defined derived characters (Polly 1994; Morlo et al. 2009, 2014; Grohé et al. 2012; Solé & Smith 2013; Solé et al. 2013, 2014; Rana et al. 2015). While †Hyaenodontidae and †Oxyaenidae share broad similarities, particularly the presence of multiple carnassial pairs, recent workers increasingly consider “Creodonta” to be para- or polyphyletic, placing hyaenodontids and oxyaenids in separate orders, Hyaenodonta† and Oyxaenodonta† (Grohé et al. 2012; Solé & Smith 2013; Solé et al. 2015). The Carnivoramorpha, Oxyaenodonta, and Hyaenodonta are distinguished based on the position of the carnassial teeth and the number of molars (Flynn & Wesley-Hunt 2005; Rose 2006). The carnassial teeth of the Carnivoramorpha are in P4 and M1, while they are located more posteriorly in the Oxyaenodonta and Hyaenodonta. Moreover, these latter groups generally possess more numerous molars than the carnivoramorphans. However, confidently resolving this issue requires a broader investigation of carnivorous Eutherian phylogeny. It is difficult to investigate the ‘creodont’ monophyly and the relationships of the two major “creodont families” (Zach et al. 2019).

Due to this uncertainty raised in the phylogenetic relationship between the clades Carnivoramorpha, Hyaenodonta, and Oxyaenodonta is that in this research, we treat the mammalian carnivores considering both scenarios: 1) the mammalian carnivores as a monophyletic group considering Carnivoramorpha as the sister clade of Hyaenodonta + Oxyaenodonta, and 2) the three groups as independent monophilies without a most common recent ancestor between them. Despite the uncertainty raised in the relationship of these three early groups, the phylogenetical relationships within Carnivoramorpha are quite stable and represent by far the most diverse clade with representatives alive today.

Currently, the mammalian carnivores are only represented by the order Carnivora, being one of the most threatened groups within vertebrates and include species at all levels of extinction risk due to a long history of interactions with hominids since the Pleistocene and contemporary global anthropogenic disturbances, those that pose a continuing threat to wildlife (Kurtén 1968; Brain 1981; Clutton-Brock 1996; Leadley et al. 2010). The clade's vulnerability and the human desire to protect it have spurred numerous efforts, strategies, and conservation plans for its many species worldwide (Cardillo et al. 2004; Loyola et al. 2008; Valenzuela-Galván & Vázquez 2008) thus allowing a broad knowledge of its natural history and occurrence sites. Carnivora also stands out and has become a major focus of research in ecology and conservation biology for many decades, largely thanks to its representatives' "charisma" attribute (Noss 1990; Albert et al. 2018; Tensen 2018). According to the Oxford Dictionary, charisma describes "the powerful quality some people have to attract and impress other people", without any reference to other organisms such as plant and animal species. However, it is increasingly used to describe species non-humans (Albert et al. al. 2018). In this sense, the "vulnerable" and "charismatic" species are among the most studied, which has allowed gathering sufficient morphological, evolutionary, ethological, and ecological information on this order in comparison to other taxa (e.g., Harris & Steudel 1997; Tseng & Flynn 2018). In addition, its fossil record is particularly rich, allowing a complete evolutionary understanding of the group (Werdelin & Turner 1996; Van Valkenburgh 1999). Related to this, Carnivora and their extinct relatives also exhibit a lower "Wallace Deficit", that is, a lack of data on the geographic distribution of the species, which has been postulated as an important historical problem in the study of biodiversity (Lomolino 2004; Hortal et al. 2015; Terribile et al. 2018; Daru 2020). Because historical biogeography, especially at large spatial scales, relies on the primary working information of the spatial distribution of the known extinct and extant species, all the above brings methodological benefits and facilitates this approach. Therefore, mammalian carnivores are an excellent model group for testing global biogeographic hypotheses and identifying patterns at large spatial and evolutionary scales (e.g., Meiri et al. 2004; Van Valkenburgh et al. 2004; Pires et al. 2015; Pires et al. 2017; Silvestro et al. 2015; Slater & Friscia 2018, 2019; Faurby et al. 2019).

Aims

This doctoral thesis aims to tell the biogeographical history of the terrestrial mammalian carnivores based on their active geographical movement across the globe, using the most complete phylogeny of the group and the largest number of geographic records for both current and extinct diversity, in and model that considers the three-dimensionality of the geographic space and the continental drift. Here, we 1) estimated the center of origin of the complete diversity of mammalian carnivores and re-write passages that, in some cases, were alleged to resolve tales about the biogeographical and evolutionary history of the group at the global scale and, 2) evaluated classical hypotheses that previously could not be evaluated at macro-scales about the link between biogeographical processes and their phenotypical evolutionary responses.

- In Chapter 1, called "*Where terrestrial mammalian carnivores originated? From early groups to the colonization of the last continent*", we estimated the center of origin and dispersal abilities of all diversity of mammalian carnivores to elucidate (contrast or support) previously proposed ideas about their biogeographical history. For this, we estimated the distances traveled and speed of movement of the lineages that join the centers of origin estimated to identify then and quantify the colonization events that allowed the origin and worldwide distribution of the complete diversity of mammalian carnivores.

- In Chapter 2, called *"How to survive on the journey: Fast body size evolution associated with long geographic dispersal in mammalian carnivores"* we use the geographical distances traveled estimated by the species to identify if they correspond to trans-continental or intra-continental dispersals and, evaluate two hypotheses to explain if this biogeographical process implies a fast evolution in body size due the selective pressures of the environment.

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CHAPTER 1: Where did terrestrial mammalian carnivores originate? From early groups to the colonization of the last continent

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ABSTRACT

The fundamental questions to understand the spatial distribution of biodiversity are where and when species originate and how they disperse over space. However, estimating the centers of origin and tracing the historical geographic paths of species has always been challenging because the fossil record, which represents direct evidence of ancestral locations, still needs to be completed, giving only the observation of scarce traces from geographically patchy evidence. In this first chapter, we used 120,694 geographical records for all species of the most complete phylogeny of mammalian carnivores to date (1,040 extinct and 277 extant species) to estimate the complete biogeographical history of the group. To do so, we used the Geographical Model that estimates the posterior distribution of longitude and latitude for each phylogenetic node while considering the spherical nature of Earth. Analyses were run, considering Hyaenodonta†, Oxyaenidae†, and Carnivoramorpha as part of monophyly. Also, these clades were considered independent monophyletic groups without an MCRA between

them. By considering the largest amount of fossil information under this new approach stand out North America as an important center of origin of early lineages, as the complete clade of mammalian carnivores, and the Oxyaenidae† and Carnivoramorpha groups. We estimate for the first time a North American origin for the order Carnivora and the subfamilies Feliformia and Caniformia. The presence of feliforms in Africa data since 10 million years before the closure of the Tethys Sea. Our results contrast with most Carnivora family's origin proposed previously by reconstructions of ancestral areas based on extant diversity. 350 of the 2632 (13.3%) distances estimated correspond to trans-continental dispersal events. Of the 350 transcontinental events, 142 are between North America and Eurasia, and 88 are between Eurasia and Africa. Twenty-three dispersal events are colonization of South America since the Middle Miocene. Interestingly, South America was initially colonized during the Middle Miocene by two distinct procyonid lineages through a process known as "island hopping." These findings challenge traditional hypotheses proposing a single lineage that arrived on the continent, followed by a six-million-year period with no further dispersals until the next wave. Thirteen monophyletic groups at the genus level (1 feliform and 12 caniforms) were estimated with an ancestral location (center of origin) in South America.

“Nevertheless, the simplicity of the view that each species was first produced within a single region captivates the mind” "Hence it seems to me, as it has to many other naturalists, that the view of each species having been produced in one area alone, and having subsequently migrated from that area as far as its powers of migration and subsistence under past and present conditions permitted, is the most probable" (Darwin 1859; Croizat et al. 1974).

INTRODUCTION

Centers of origin

The "unique origin of life" is one of the most important ideas regarding the origin of biodiversity and its expressions in time and space. This idea scales to any complexity or taxonomic level (even to individual levels), where each level follows the same pattern in which new life forms originated from a common ancestor (Darwin 1859). However, where and when did each ancestor and their respective descendants originate? How did they disperse over space and throughout new environments on Earth to reach their present (or past) distribution? These are part of the fundamental questions to understand the spatial distribution of biodiversity, and they have encouraged researchers for decades to infer the events from the deep past. By examining these questions through the lenses of ecology, evolution, biogeography, geology, and paleontology, and focusing on low taxonomic and spatiotemporal scales, we have pieced together a historical puzzle. This has enabled us to shed light on a phenomenon that converges at a common space-time point and has diversified as it disperses over geographical space. This has become a major goal of biogeography and comparative biology, in which researchers infer where the ancestors of a particular clade occurred, i.e., they try to discover the centers of origin (Croizat et al.1974; Bremer 1992; Goldberg et al. 2005; Dupin & Smith 2019; Morrone 2020; Wisniewski et al. 2022).

The concepts of “centers of origin” and “dispersal” are deeply ingrained in biogeographic thoughts, and they are applied to the species level (Olson 1971). The concept of center of origin has been defined classically as a "limited area" in which a "few ancestors" of a species may be supposed to have originated, and from which the species may be supposed to have dispersed to achieve its present distribution (Udvardy 1969; Croizat et al. 1974). Now, according to the macroevolutionary and biogeographical context of this research, we define "dispersal" as the geographic movement of "species" from its center of origin, under the understanding that a "species" corresponds to a metapopulation lineage evolving independently of another metapopulation lineage (De Queiroz 2007). However, estimating the centers of origin and tracing the historical paths of species is a challenging task because, while we can be reasonably confident in the current distribution of many taxa, it is challenging to infer where ancestral species and extinct species occurred in the past. In this sense, recent evidence shows that a clade's past geographical range (or center of origin) cannot be accurately inferred with data from extant taxa alone (Archibald 2003; Lieberman 2003; Silvestro et al. 2016; Wisniewski et al. 2022). The fossil record represents crucial, albeit incomplete, information to estimate these ancestral locations and trace the potential historical dispersal pathways of species, corresponding to the observation of scarce traces that help to explain how present spatial patterns were shaped from geographically distant evidence (Sanmartín et al. 2008; Crisp et al. 2011; Matzke 2013; Antonelli et al. 2015; Meseger et al. 2015; Silvestro et al. 2016; Gardner et al. 2019). However, the fossil record has the inherent limitations of temporal bias, taxonomic bias, spatial bias, and identification problems (Smith 2001; Benson et al. 2010; Gardner et al. 2019; Hoban 2019). For example, species diversity increases with time due to fossils' preferential preservation and recovery in younger geological strata, a phenomenon known as "the Pull of the Recent" (Jablonski et al. 2003).

To overcome these limitations, currently, biogeographers use complementary approaches combining these different lines of evidence as molecular phylogenies and fossil records, obtaining a complete and more accurate picture of biogeographic processes and patterns. Although those approaches can work with both kinds of data, their model assumptions have some limitations. These models assume that species "jump" between the discrete geographical areas previously defined (generally, continents or bioregions) without considering the three-dimensionality of the geographic space and the continental drift (Ronquist 1997; Ronquist 2001; Ree et al. 2005; Ree & Smith 2008; Matzke 2013). Therefore, the use the extinct and extant diversity and their phylogenetical relation in a model that allows the free estimation of ancestral locations and displacement considering the continuous nature of the geographical data could help to unclear the biogeographical history of biodiversity to deep scales, even re-write passages of tales that in some cases were alleged to be resolved.

Joining points for a unique and branched journey

The early dispersal history of terrestrial mammalian carnivores has a complex and fast dynamic across northern landmasses, which has made it difficult to estimate the center of origin of these ancient lineages (Van Valkenburgh 1999; Pires et al. 2015; Borths et al. 2016; Faurby et al. 2019). Additionally, the fact that most works evaluate the biogeographic origin and dispersal of specific groups without connecting the spatial points to a single and complete biogeographic history adds more complexity to discovering those deep biographical patterns. Moreover, the phylogenetic relationship between mammalian carnivores has been recently questioned (Solé & Smith 2013) given a new hypothesis obtained from phylogenetic studies that include ‘creodonts’ (Hyaenodonta† + Oxyaenidae†) and carnivoramorphans (Carnivoraformes + Viverravidae†). This has made it hard to understand whether mammalian carnivores had a unique or more independent biogeographical history. In this sense, Solé & Smith (2013) suggested distinct centers of origin for the mammalian carnivores (Oxyaenidae†, Hyaenodonta†, and Carnivoramorpha), resulting in independent biogeographical histories. A recent work that treats mammalian carnivores as a monophyletic group estimated a unique origin in North America (Faurby et al. 2019). A North American origin has also been proposed for Oxyaenidae† (Chester et al. 2010; Faurby et al. 2019), an Afro-Arabian (Solé et al. 2009) or European (Borths et al. 2016) origin for Hyaenodonta†, and a Eurasian (Solé et al. 2016) or North American (Faurby et al. 2019) origin for Carnivoramorpha. Mammalian carnivores were absent from the African landscape for the early periods of the Cenozoic, and the Hyaenodonta† clade was the first group to occupy the carnivore niches in this continent (Rose 2006; Wederlin & Sanders 2010; Borths et al. 2016; Mattingly et al. 2020).

Within Carnivoramorpha, Carnivora represents the only living clade of all mammalian carnivores, grouping 296 extant species distributed across all continents (Hassanin et al. 2021) and whose origin has been proposed in high-latitudes (Rolland et al. 2015) and/or Eastern Eurasia during the early Paleogene (Solé et al. 2016), whit posterior high dispersal rate from high to low latitudes. Similarly, based on extant diversity, Feliformia and Caniformia suborders have been estimated to have an origin in eastern Eurasia (Rolland et al. 2015; Zhou et al. 2017). Most extant feliform families have moved southward (Barycka 2006; Pedersen et al. 2014), with ancestors estimated in an uncertain location (Rolland et al. 2015) or Eurasia (Zhou et al. 2017) for Viverridae family; Eurasia for Felidae and Prionodontidae families (Johnson et al. 2006; Pires et al. 2015; Zhou et al. 2017); and Africa for Hyaenidae, Herpestidae and Nandiniidae families (Rolland et al. 2015; Zhou et al. 2017). Also, Malagasy carnivorans, i.e., the Eupleridae family, has been proposed as a monophyletic and thus the product of a single colonization of Madagascar by an African ancestor (Yoder et al. 2003; Barycka 2006; Rolland et al. 2015; Zhou et al. 2017). Concerning extinct feliform families, Nimravidae was recently estimated with an uncertain origin in Asia or North America (Barrett et al. 2021), and Barbourfelidae was estimated with an origin in Eurasia (Pires et al. 2015; Barrett et al. 2021). Only the Felidae family reached South America (Eizirik 2012; Prevosti & Forasiepi 2018). On the other hand, from the potential Eurasian origin of Caniformia, the Mephitidae family has also been proposed with an origin in Eurasia (Pires et al. 2015). The families Ailuridae, Amphicyonidae, Canidae, and Ursidae were estimated to an origin in North America (Wolsan & Lange-Bradré 1996; Wang & Tedford 2008; Prothero 2013; Pires et al. 2015; Rolland et al. 2015). Mustelidae and Procyonidae families have been proposed with a North American (Pires et al. 2015; Rolland et al. 2015) or Eurasian (Koepfli et al. 2008; Sato et al. 2012; Pires et al. 2015) origin with posterior multiple dispersal events to Africa and South America. Then, due to the extensive isolation period and the lack of early lineage fossils, it is a fact that South America was the last continent to be colonized by Carnivora (Simpson 1980; Webb 1985; Woodburne 2010; Forasiepi et al. 2014). Of the 13 extant terrestrial carnivoran families, only six are present in South America: Felidae, Canidae, Mustelidae, Mephitidae, Procyonidae, and Ursidae (Prevosti et al. 2012; Pino et al. 2022), showing that the colonization of the continent has been in several independent events associated to the Great American Biotic Interchange (GABI) and its previous steps (Cione et al. 2015; Ruiz-García et al. 2022). Despite their recent history in the continent, an amazing (endemic?) species diversity has originated. However, we do not know whether this diversity comes from ancestral species originating in South America (Ruiz-García et al. 2022).

Considering the background presented, in this first chapter we answer the question, where did terrestrial mammalian carnivores originate? and we take the previous proposals based on the fossil record and/or extant diversity as biogeographic hypotheses. We use the available geographic data for extinct and extant diversity and the most complete phylogeny to estimate the complete biogeographical history of terrestrial mammalian carnivores. In specific:

1) We elucidate (to contrast or support) the previously proposed ideas about the center of origin of the group and their early and recent lineage descendants.

2) We estimate the distances traveled and speed of movement of the lineages that join the centers of origin estimated.

3) We identify the first colonization event towards the different continents and quantify the number of dispersal events, emphasizing the South American biogeographical history, the last continent to be colonized.

METHODS

Phylogeny

In order to cover a complete biogeographic framework regarding the place and time of origin for mammalian carnivores and all their subclades, this research was conducted on a recent phylogeny of the group that considers the extant diversity and a vast extinct diversity (Faurby et al. 2019). This phylogeny consists of a sample of 1,000 trees, including 1,713 tips, both extinct and extant mammalian carnivores. Specifically, the phylogeny includes 198 extinct species of Hyaenodonta† and Oxyanidae† and 1,515 Carnivoramorpha species (Carnivoraformes + Viverravidae†). 314 species are extant and belong to the Carnivora order. This is the first species-level phylogeny of mammalian carnivores, including all suitable fossils and extant species. To infer the locations of all ancestral species, using the Geographical (Geo) model (see below), we used a Maximum Clade Credibility (MCC) tree, constructed from the posterior sample trees. We modified 144 branches of fossil species with 0 lengths to run the Geomodel analysis. We assigned near-zero branch length (0.000001) to ensure that the Geomodel analysis will not modify the branch so that the estimated location fossil ancestral node is at the fossil location with high accuracy and precision (Avaria-Llautureo et al. 2021). Additionally, several species were removed from the phylogeny. First, *Miacis uintensis*, *Uintacyon major*, *Mustela* *larteti*, *Schlossericyon viverroides,* and *Stenogale aurelianensis* were removed because they were discovered to be junior synonyms (Faurby et al. 2021). Second, we removed one of the sister species when both had the exact and single geographic coordinates. Third, we removed Pinnipedimorpha clade because we aim to estimate the biogeographical history of terrestrial mammalian carnivores. Thus, the final phylogeny as input to Geomodel analysis contains 1,317 species (1040 extinct and 277 extant). Finally, due to the phylogenetic uncertainty raised in the relationship of the three early clades, we ran analyses using the complete phylogeny (1317 species), and for the three groups separately: Carnivoramorpha (1141 species), Hyaenodonta† (150 species), and Oxyaenidae† (26 species).

Geographic data

We obtained the geographic locations from different databases for each species, both extant and extinct in the phylogeny. For extinct species, we obtained the cartesian coordinates (longitude and latitude) mainly from the "Paleobiology Database" (PBDB; Peters & McClennen 2016). We downloaded and cleaned these fossil occurrence data using the “clean_fossils” function from the “CoordinateCleaner” R package. This function runs multiple empirical tests to identify occurrences with potentially erroneous coordinates and erroneous fossil ages (Zizka et al. 2019). Coordinates of extinct species absent in this database were obtained from specific literature, mainly from each fossil description paper. In these cases, we estimated the paleo coordinates from the present-day coordinates (fossil deposits) location based on the PALEOMAP model, which is implemented in the function "reconstruct" of the "choronosphere" R package (Kocsis & Raja 2020). For extant species, the neotropical records of Nagi-Reis et al. (2020) were preferred due to their updated compilation and systematization of records from different data sources. We obtained geographic coordinates from the GBIF database for the rest extant species. We used the protocol of Rolland et al. (2018) to download and clean the GBIF records. Finally, records for each extant species overlapped with their respective distribution map available in IUCN red list to erase records outside the actual distribution. Then, we applied several additional filters to data records before the definitive analyses. First, duplicated coordinates between sister species were removed as the Geomodel collapsed the branch lengths of sister species to zero when they duplicated data. Then, a random sample of 3,000 coordinates was obtained for those species with more than 3,000 geographic records. This is because previous tests showed that more records do not improve the estimations and only delay the analysis. Finally, our dataset contained 120,694 records for the 1317 tips of the phylogeny. From this dataset, two input files for Geomodel analysis were generated, one that considers all the species in the phylogeny, i.e., species that have only one record (i.e., the centroid from the sample of coordinates or single occurrence data), and a second file that contains multiple records for species.

Centers of origin and dispersal ability (geographical distance and speed of movement)

We inferred the paleo-distribution of all common ancestors in a three-dimensional continuous space using the geographic locations within each species as input data. Each phylogenetic node's ancestral locations were estimated using the Geomodel (O'donovan et al. 2018) in the computer program BayesTraits 4.0 (Pagel et al. 2004). The model estimates the posterior distribution of ancestral locations measured in longitude and latitude while sampling across all location data within species and considering the spherical nature of Earth. These estimations are based on the variable-rates model (Venditti et al. 2011), which detects shifts away from a background rate of evolution in continuous traits (expected under BM) in whole clades or individual branches. In order to consider the tectonic drift, the paleo-distribution of the ancestors was estimated considering paleo maps that represent the configuration of the continents in the node's age. Seventeen maps with the continental configuration every 5 million years, from the present to 80 million years ago, were used. These maps were obtained from the PALEOMAP PaleoAtlas for GPlates (Scotese 2016). This allows the ancestral locations estimated to match the geographical position of the land masses at that moment. In addition, it was restricted that each estimate is within the land masses, preventing estimates located in the sea. We ran four MCMC chains for 300,000,000 iterations, sampling every 50,000 iterations and discarding 250,000,000 as burn-in. The chain convergence was checked using the effective sample size (ESS) in Tracer v.1.7.1, ensuring outputs with ESS > 200. The final sample includes 1,000 posterior locations for each phylogenetic node. From Geomodel outputs, each lineage's geographic distance historically dispersed across each phylogenetic branch (branch-wise distances) was calculated. Then, these distances were summed along the path that links the root with tips (pathwise distances). The "branch-wise distances" were calculated using the "distCosine" function in the "geosphere" R package (Hijmans 2019). The distCosine function brings the shortest distance between two points, assuming a spherical Earth. To obtain the historical distance dispersed for each species and considering the uncertainty in ancestral locations estimates, the “branch-wise distances” for every one of the 1000 locations estimated were calculated in the posterior sample and, therefore, 1000 "pathwise distances" for each species in the phylogeny were obtained. Also, since we have a time-calibrated phylogeny, the Geomodel analysis simultaneously estimates the speed of species movement across each branch that links pairs of phylogenetic nodes. Thus, the "branch-wise speed of movement" was calculated in km Myr–1, dividing the branch-wise distances (in kilometers) by the branch length (in million years) of the MCC time-calibrated tree. We obtained two new phylogenies where each branch was scaled by the geographical distance of movement and the speed of movement estimated, respectively. Finally, given that each branch represents a dispersal event with a respective geographical distance estimated between its ancestral node and its descendant node, we identify and quantify the trans-continental and intra-continental dispersal events.

RESULTS

Centers of origin

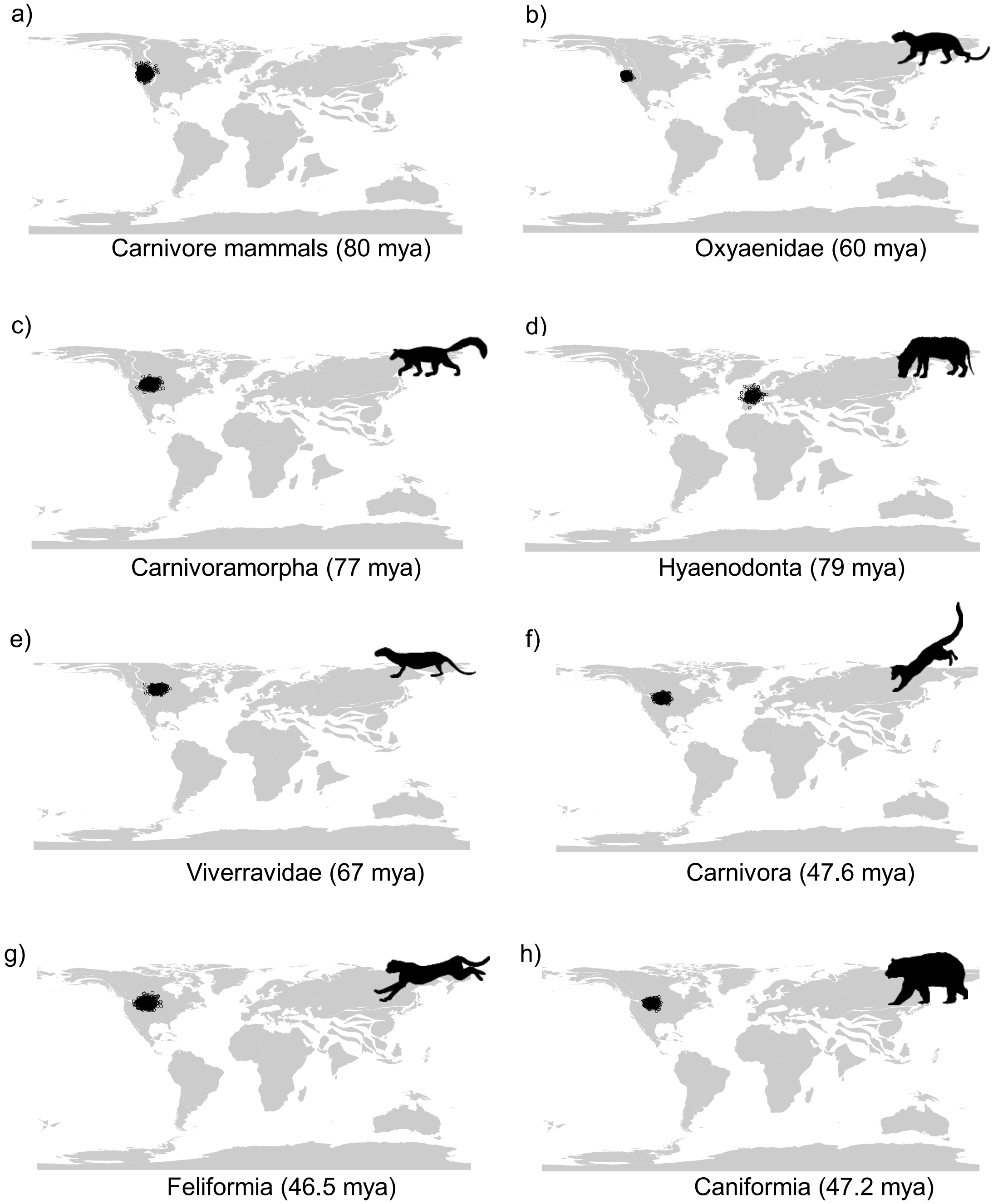
The highest posterior density (HPD, 780 from 1000 coordinates in the posterior sample) using the complete phylogeny shows that the ancestral location (center of origin) of all mammalian carnivores and early groups, i.e., Oxyaenidae†, Hyaenodonta†, and Carnivoramorpha were strongly estimated in North America. When analyses were run for each early group as independent monophylies, results were qualitatively similar for

Oxyaenidae†, Carnivoramorpha, and their internal lineages (Table 1). In specific, for Oxyaenidae† phylogeny, the highest posterior density (i.e., 780 samples equal to 95% CI) show an ancestral location (center of origin) in North America with a median value estimated very close to previous analysis (Long = -109.163; Lat: 44.066 vs Table 1; Figure 1b). For Carnivoramorpha phylogeny, the analysis shows that the ancestral location is in North America with a median value estimated very close to the previous analysis (Long = - 79.321; Lat = 53.449 vs Table 1; Figure 1c). Clades within Carnivoramorpha do not show changes in their ancestral geographical location. However, for Hyaenodonta†, the center of origin changed. For Hyaenodonta† phylogeny, the highest posterior density (i.e., 780 samples equal to 95% CI) show an ancestral location in Europe, contrary to the estimate using the complete phylogeny of carnivore mammals (Long = 0.677; Lat = 41.121). To resolve this, we ran a third analysis over the complete phylogeny but with the Hyaenodonta† origin constrained to Europe. According to marginal likelihood, the most probable model shows an origin in Europe (Lik: -6802.863958; Figure 1d) compared to North America (Lik: -6826.191742).

Table 1. Ancestral locations estimated for main mammalian carnivores' clades over family taxonomical category. The Long and Lat columns correspond to the median value of 780 posterior coordinates.

Clade	N° species	Age	Long	Lat	Current continent
Mammalian carnivores	1317	80	-105.212	45.737	North América
Hyaenodonta†	150	79	0.677	41.121	Europe
Oxyaenidae†	26	60	-108.721	44.456	North América

Carnivoramorpha	1141	77	-88.556	50.307	North América
Viverravidae†	24	68	-80.308	53.118	North América
Carnivora	1080	47	-89.811	47.745	North América
Feliformia	372	46	-89.678	48.034	North América
Caniformia	708	47	-89.852	47.754	North América



Carnivore mammals (80 mya)

Oxyaenidae (60 mya)

Carnivoramorpha (77 mya)

Hyaenodonta (79 mya)

Viverravidae (67 mya)

Carnivora (47.6 mya)

Feliformia (46.5 mya)

Caniformia (47.2 mya)

Figure 1. Posterior coordinates represent the ancestral locations for main mammalian carnivores' clades over the family taxonomical category. The posterior distribution of ancestral locations is represented as a

density plot of the 780 (95% CI) samples of MCMC chains. Black silhouettes of species were obtained from PhyloPic.

Also, within Carnivoramorpha, the ancestral location of the MCRA for Viverravidae†, Carnivora, Feliformia, and Caniformia, was strongly estimated across North America as well (Table 1; Fig. 1 e-h). Then, within the Carnivora order, and belonging to Feliformia suborder: the MCRA of Nimravidae† and the polyphyletic Stenoplesictidae† families were estimated in North America; The MCRA of Nandiniidae, Herpestidae, Viverridae, and Barbourofelidae† families were estimated in África; Hyaenidae and Felidae families in Europe; Eupleridae family in Madagascar; Prionodontidae family in Asia and; Percrocutidae† shows uncertainty between an origin in Europe or Africa (Table 2; Fig. 2 a-k); belonging to Caniformia suborder: the MCRA of most families were estimated in North América: Amphicyonidae†, Canidae, Ursidae, Procyonidae, and Mustelidae; however, Ailuridae and Mephitidae families were estimated in Europe (Table 2; Fig. 2 l-q).

Table 2. Ancestral locations estimated for all families of Carnivora order. The Longitude and Latitude correspond to the median value of 780 posterior coordinates.

Clade	N° species	Age	Long	Lat	Current continent
Feliformia					
Nimravidae†	14	46.3	-89.688	48.041	North América
Nandiinidae	1	38	29.155	1.255	África
Stenoplesictidae†	9	35.8	-80.128	49.186	North América
Herpestidae	56	30.2	28.554	14.811	África
Felidae	114	29.4	11.088	43.617	Europe
Viverridae	65	28.2	31.685	5.457	África
Barbourofelidae†	14	21.5	32.031	0.329	África
Hyaenidae	68	17.5	20.733	42.449	Europe

Eupleridae	11	17.5	45.529	-16.811	Madagascar
Percrocutidae†	11	17.4	37.034	24.745	África / Europe
Prionodontidae	2	6.9	98.909	17.651	Southeast Asia
Caniformia					
Amphicyonidae†	95	44.6	-88.667	48.172	North América
Canidae	201	42.9	-89.964	47.681	North América
Ursidae	91	42	-88.081	49.191	North América
Procyonidae	41	33.1	-86.683	50.342	North América
Ailuridae	13	28.8	7.924	49.288	Europe
Mustelidae	229	28.1	-92.816	47.373	North América
Mephitidae	36	21.7	11.322	48.624	Europe

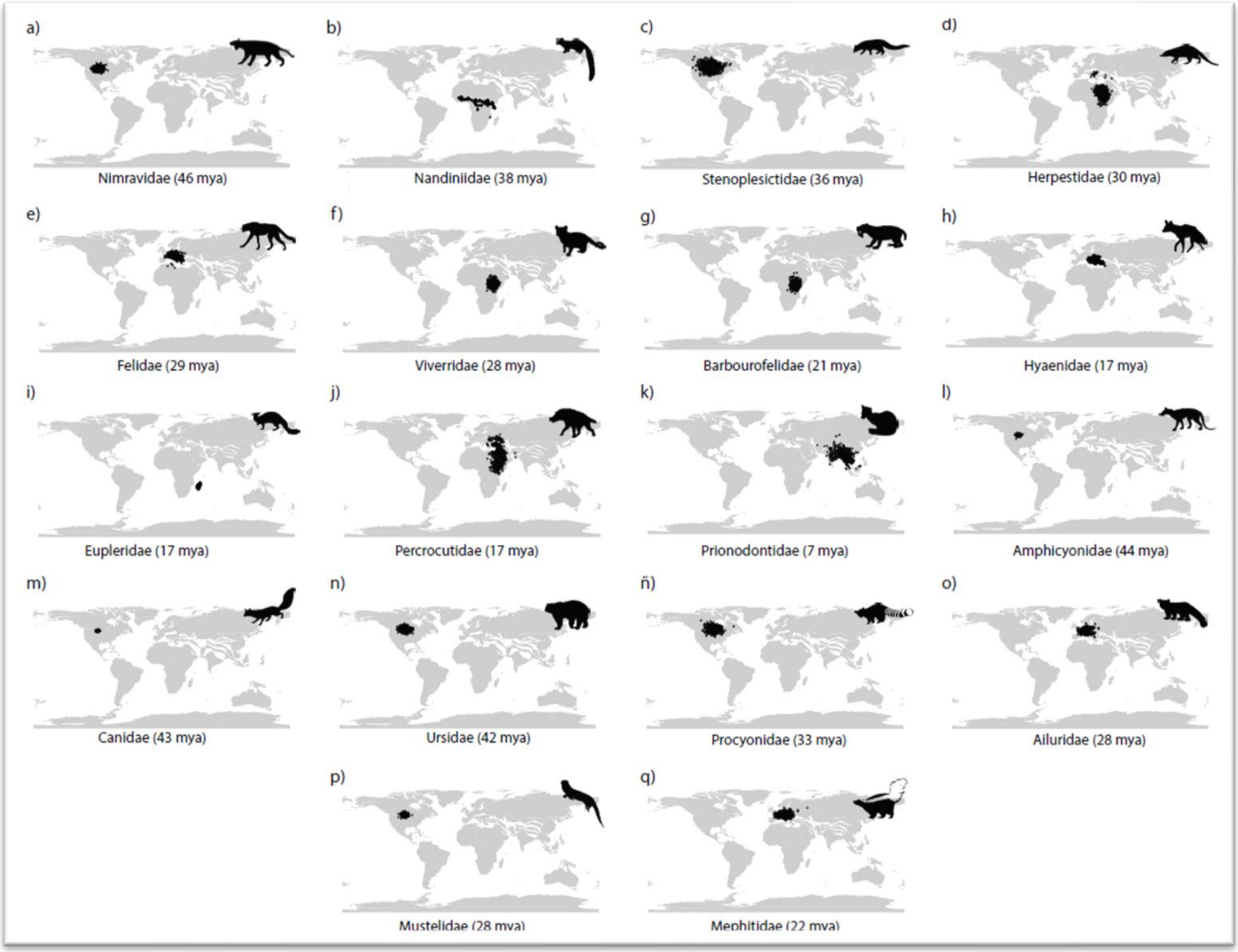


Figure 2. Ancestral location estimated for families of Carnivora order. Ancestral locations are drawn as a density plot of the 780 (95% CI) samples of MCMC chains. Black silhouettes of species were obtained from PhyloPic.

Table 3. Comparison of centers of origin of this study and previous ones

Clade	Latest studies	Method	Reference	This study
Hyaenodonta†	Afro-Arabia / Europe / North America	Fossil record / Ancestral states in RASP / DEC in BiogeoBEARS	Solé et al. 2009 / Borths et al. 2016 / Faurby et al. 2019	Europe
Oxyaenidae†	North America	Fossil record / DEC in BiogeoBEARS	Chester et al. 2010; Faurby et al. 2019	North America
Carnivoramorpha	Asia / North America	Fossil record / DEC in BiogeoBEARS	Solé et al. 2016 / Faurby et al. 2019	North America

Carnivora	Asia	Lagrange and DEC / Fossil record	Rolland et al. 2015 / Solé et al. 2016	North America
Feliformia	Asia	Lagrange and DEC in BioGeoBEARS	Rolland et al. 2015	North America
Nimravidae †	Asia or North America	DIVALIKE + J model of BioGeoBEARS	Barrett et al. 2021	North América
Nandiinidae	África	Lagrange and DEC in BioGeoBEARS	Rolland et al. 2015; Zhou et al. 2017	África
Stenoplesictidae †	-	-	-	North América
Herpestidae	África-India	Lagrange and DEC in BioGeoBEARS	Rolland et al. 2015; Zhou et al. 2017	África
Felidae	Eurasia / South Asia	Bayesian approach to estimate speciation and extinction rates from fossil occurrences data / Lagrange	Pires et al. 2015; Zhou et al. 2017	Europe
Viverridae	Eurasia	Lagrange	Zhou et al. 2017	África
Barbourofelidae†	Europe / Eurasia	DIVALIKE + J model of BioGeoBEARS / Bayesian approach to estimate speciation and extinction rates from fossil occurrences data	Barret al. 2021 / Pires et al. 2015	África
Hyaenidae	África	Lagrange and DEC in BioGeoBEARS	Rolland et al. 2015; Zhou et al. 2017	Europe
Eupleridae	Madagascar	Lagrange and DEC in BioGeoBEARS	Rolland et al. 2015; Zhou et al. 2017	Madagascar
Percrocutidae†	-	-	-	África / Europe
Prionodontidae	Southeast Asia	Lagrange and DEC in BioGeoBEARS	Rolland et al. 2015; Zhou et al. 2017	Southeast Asia
Caniformia	Asia	Lagrange and DEC in BioGeoBEARS	Rolland et al. 2015	North América
Amphicyonidae†	North America	Bayesian approach to estimate speciation and extinction rates from fossil occurrences data	Pires et al. 2015	North América
Canidae	North America	Bayesian approach to estimate speciation and extinction rates from fossil occurrences data	Pires et al. 2015	North América
Ursidae	North America	Bayesian approach to estimate speciation and extinction rates from fossil occurrences data	Pires et al. 2015	North América
Procyonidae	Eurasia	Bayesian speciation and extinction rates from fossil occurrences data	Pires et al. 2015	North América
Ailuridae	North América	Lagrange and DEC in BioGeoBEARS	Rolland et al. 2015	Europe
Mustelidae	Asia / North América	Bayesian model-averaging approach in BayesTraits / Bayesian approach to estimate speciation and extinction rates from fossil occurrences data; Lagrange and DEC in BioGeoBEARS	Sato et al. 2012 / Pires et al. 2015; Rolland et al. 2015	North America
Mephitidae	Eurasia	Bayesian	Pires et al. 2015	Europe

Distance traveled and speed of historical dispersal events.

For mammalian carnivores, the geographic analyses support a model with significant variation in the distance traveled across phylogenetic branches, ranging from 0.01 to 15,077 kilometers (Fig. 3a). The speed of movement per phylogenetic branch ranged from 0.02 to 94,177 kilometers per million years (Fig. 3b). 350 of 2,632 (13.3%) distances estimated correspond to trans-continental dispersal events. Therefore, most of the estimated dispersal events (86.7%) correspond to the movement of lineages inside the continental landmasses. Of the 350 transcontinental events, 112 are between North America and Europe, 30 between North America and Asia, 85 between Europe and Asia, 62 between Europe and Africa, 26 between Africa and Asia, 25 between North America and South America, and 10 are rare, i.e., between continent without geographical connections. On average, the longest (9,887 kilometers) and fastest (10,051 km/my) dispersal distances estimated between continents are rare, followed by North America – Asia with 8,504 and 3,947 km/my estimated. The shortest (4,194 km) and slowest (2253 km/my) are between Europe and Africa. Oxyaenidae†, Hyaenodonta†, and Carnivoramorpha show a similar pattern of high density of short-traveled distances estimated with a gradual decrease in the density towards long-traveled distances estimated (Figure 3c). In this sense, Oxyaenidae† accumulated the highest density of short-traveled distances estimated because their diversity was distributed constrained mainly to North

America with two peaks of long-traveled distances. On the other hand, Carnivoramorpha showed the most homogeneous distribution with a lower density of short distance compared to the other two groups and a flatted decrease distribution towards middle and long distances estimated (Figure 3c). This is related to the movement of lineages across all continental landmasses, including South America. Then, inside Carnivoramorpha, most families have the highest density of distance traveled between 500 and 2,000 km. Barbourofelidae† (Feliformia) and Amphicynodontidae† (Caniformia), both extinct, are the families with the highest density of long-distance dispersion (Figure 3e). Regarding the speed of movement across lineages, Oxyaenidae†, Hyaenodonta†, and Carnivoramorpha showed a similar pattern of the high density of low speeds of movement estimated (between 0 and 1,250 km/my) with a decrease in the density towards high speeds of movement. In this sense, Carnivoramorpha shows the widest and most homogeneous distribution with a flatted decrease distribution towards high speeds of movement estimated (Figure 3d). Then, inside Carnivoramorpha, most families have the highest density between 0 and 2,000 km/My of speed. Nimravidae† and Barbourofelidae† are feliform families with higher values of speed of movement estimated. While Mephitidae and Ailuridae families (caniforms) show higher speed of movement estimated (Figure 3f).

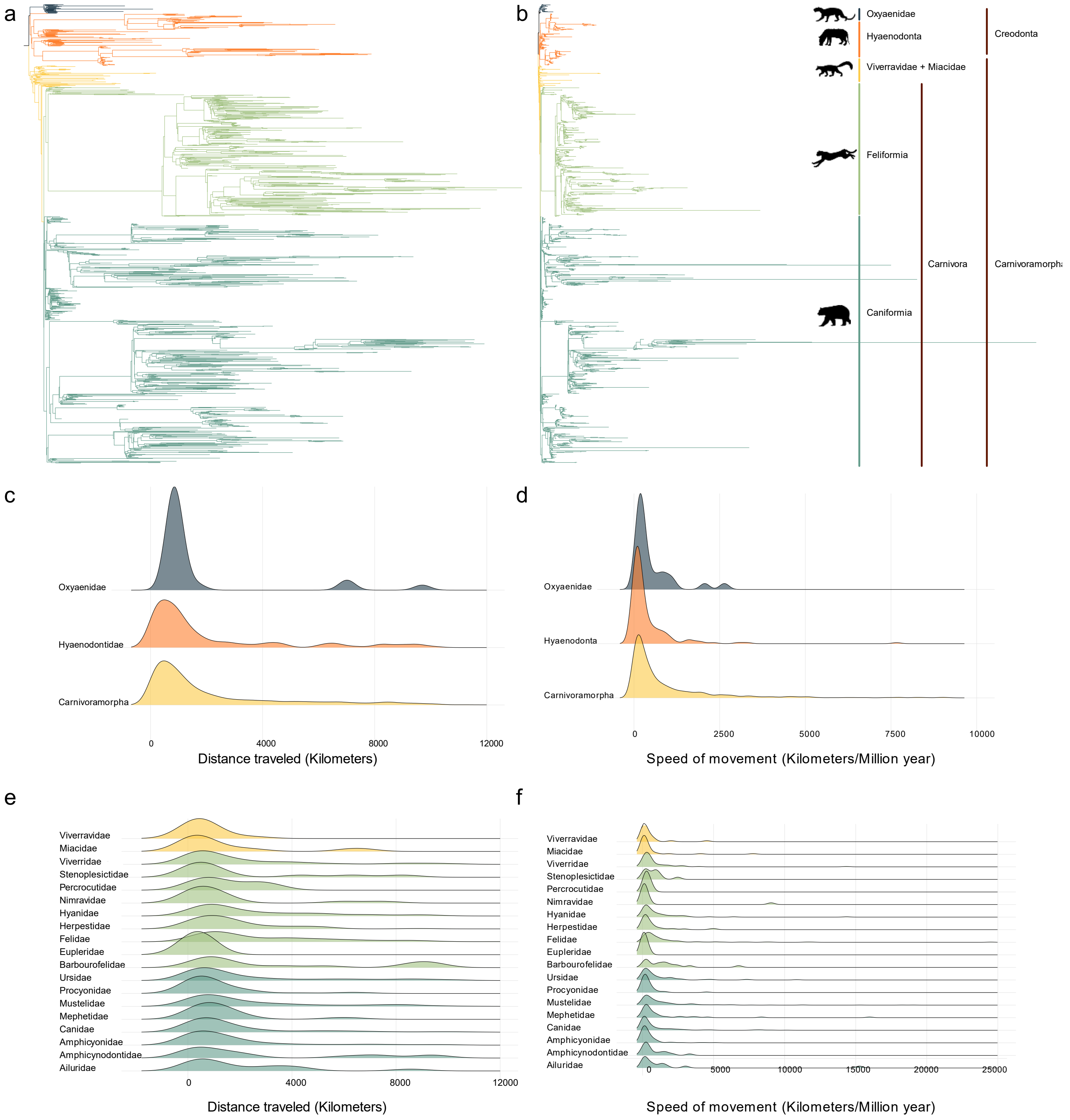

a
b
Oxyaenidae
Hyaenodonta
Viverravidae + Miacidae
Creodonta
Feliformia
Carnivora
Carnivoramorph
Caniformia
c
Oxyaenidae
Hyaenodontidae
Carnivoramorpha
0
4000
8000
12000
Distance traveled (Kilometers)
d
Oxyaenidae
Hyaenodonta
Carnivoramorpha
0
2500
5000
7500
10000
Speed of movement (Kilometers/Million year)
e
Viverravidae
Miacidae
Viverridae
Stenoplesictidae
Percrocutidae
Nimravidae
Hyanidae
Herpestidae
Felidae
Eupleridae
Barbourofelidae
Ursidae
Procyonidae
Mustelidae
Mephetidae
Canidae
Amphicyonidae
Amphicynodontidae
Ailuridae
0
4000
8000
12000
Distance traveled (Kilometers)
f
Viverravidae
Miacidae
Viverridae
Stenoplesictidae
Percrocutidae
Nimravidae
Hyanidae
Herpestidae
Felidae
Eupleridae
Barbourofelidae
Ursidae
Procyonidae
Mustelidae
Mephetidae
Canidae
Amphicyonidae
Amphicynodontidae
Ailuridae
0
5000
10000
15000
20000
25000
Speed of movement (Kilometers/Million year)

Figure 3. Distance traveled and speed of movement estimated by Geomodel analysis: a) phylogenetic tree scaled by traveled distance (branch length is kilometers); b) phylogenetic tree scaled by the speed of movement (branch length is kilometers/million year); c) Distance traveled estimated by early groups; d) Speed of movement estimated by early groups; e) Distance traveled estimated by Carnivora families; f) Speed of movement estimated by Carnivora families. Black silhouettes of species were obtained from PhyloPic.

For Oxyaenidae†, from their center of origin in western North America (Table 1, Figure 1b) in the Late Paleocene (60 million years ago), 52 dispersal events were estimated: 49 dispersal events inside North America and three correspond to trans-continental events: two towards Europe where "*Oxyaena woutersi*" and "*Palaeonictis gigantea*" originated, and one to Asia where "*Sarkastodon mongoliensis*" was originated (Figure 4). These three occurred between the Early and Middle Eocene and are the longer and faster dispersal events estimated for the group with more than 6,900 kilometers traveled by the lineages at a speed of over 860 km/my (Figure 3c-d).

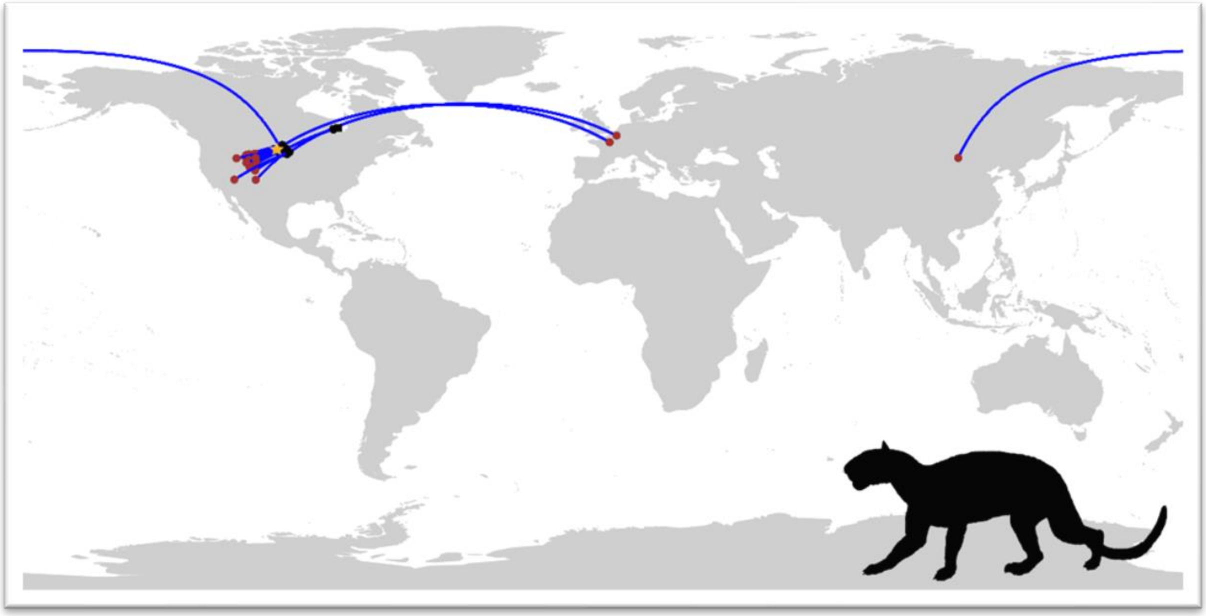


Figure 4. Biogeographic history of Oxyaenidae†. The yellow star represents the median value of the center of origin estimated. Black dots are the nodes and red dots are the tips. Blue lines are the dispersal travel estimated (shortest distance) between an ancestral and descendant node.

For Hyaenodonta†, from their center of origin in Europe (Table 1, Figure 1d) in the Late Cretaceous (76 million years ago), 300 dispersal events were estimated: 262 dispersal events inside continental landmasses and 38 correspond to trans-continental events (Figure 5). 22 transcontinental events between North America and Eurasia (in both ways) occurred from the Early Paleocene (66 mya) to Middle Miocene (12 mya). On average, the movement of lineages from North America to Eurasia was faster (1,856 km/my) than from Eurasia to North America (915 k/my). Also, six events correspond to the colonization of Africa since 62 mya (Middle Paleocene) and three to return to Eurasia.

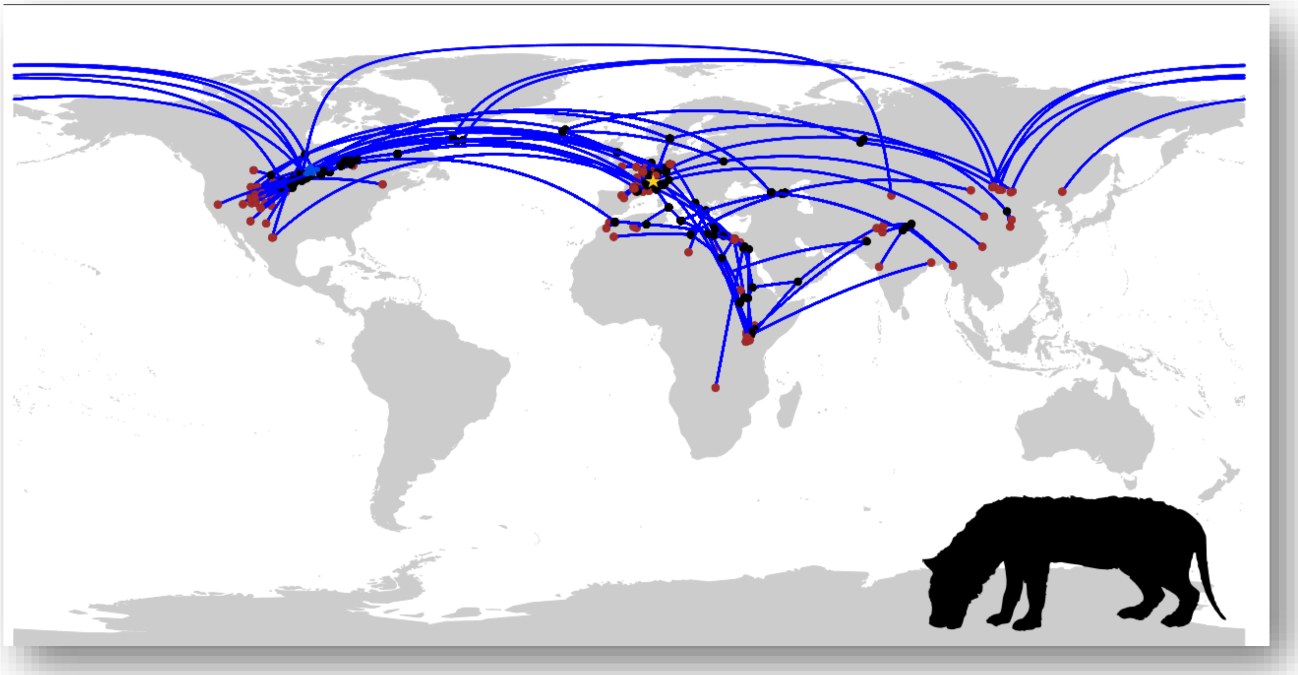


Figure 5. Biogeographic history of Hyaenodonta†. Yellow stars represent the median value of the potential centers of origin estimated. Black dots are the nodes and red dots are the tips. Blue lines are the dispersal travel estimated between an ancestral and descendant node.

For Viverravidae† (Carnivoramorpha), from their center of origin in North America (Table 1, Figure 1e), 48 dispersal events were estimated and only one corresponds to a trans-continental event toward Asia (Figure 6), in the Early Paleocene (63 mya), where the genus *Pappictidops* was originated. This event is the longer (9,507 km traveled) and faster (15,091 km/my) estimated for the group.

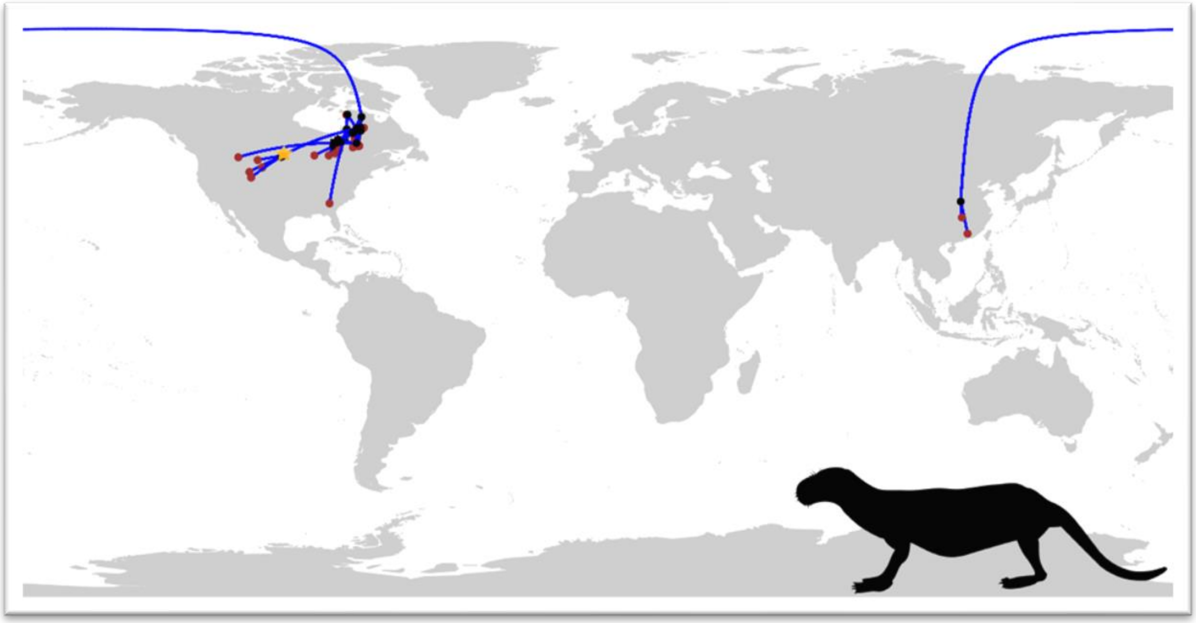


Figure 6. Biogeographic history of Viverravidae†. The yellow star represents the median value of the center of origin estimated. Black dots are the nodes and red dots are the tips. Blue lines are the dispersal travel estimated between an ancestral and descendant node.

For Carnivora order, from their center of origin in North America (Table 1, Figure 1f), 2,188 dispersal events were estimated and 431 (19.7%) correspond to trans-continental dispersal events. 113 are dispersals between North America and Eurasia: 45 from North America to Eurasia since Middle Eocene (42 mya) and 68 from Eurasia to

North America since Late Oligocene (25 mya). On average, the movement of lineages from Eurasia to North America was faster (4,239 km/my) than from North America to Eurasia (3694 km/my). 53 events were estimated as colonization towards Africa since Middle Eocene (39 mya) and 29 as dispersal from Africa to Eurasia since Late Eocene (31 mya). On average, the movement of lineages from Eurasia to Africa was faster (4,100 kilometers/million years) than from Africa to Eurasia (3,507 kilometers/million years). Inside each suborder, Feliformia arrives in Eurasia 42 mya (Middle Eocene), Africa 39 mya (Middle Eocene), and South America 7 mya (Late Miocene); while Caniformia arrives in Eurasia 32 mya (Early Oligocene), Africa 23 mya (Early Miocene) and South America 16 mya (Middle Miocene).

The last continent: The South American biogeography

Of the 2,632 estimated dispersal events, 23 are colonization events in South America since Middle Miocene (16 mya). All these events correspond to over 3,500 kilometers traveled between the ancestral node located out South America and the descendant South American lineage. Three of these events are lineages with dispersal estimated from Europe to South America: *Pteronura brasiliensis* (Mustelidae), *Eira barbara* (Mustelidae), and *Panthera onca* (Felidae); one from Asia: MCRA of the South American *Lontra* species (Mustelidae), and 19 from North America. 13 monophyletic groups at the genus level (1 feliform and 12 caniforms) were estimated with an ancestral location in South America: *Leopardus* (Felidae), *Lycalopex* (Canidae), *Atelocynus* (Canidae), *Chrysocyon* (Canidae), *Dusicyon*† (Canidae), *Galictis* (Mustelidae), *Lyncodon*

(Mustelidae), *Nasuella* (Procyonidae), *Nasua* (Procyonidae), *Bassaricyon* (Procyonidae), the *Cyonasua*-group† (*Cyonasua* and *Chapalmalania* genera; Procyonidae) and *Arctotherium*† (Ursidae).

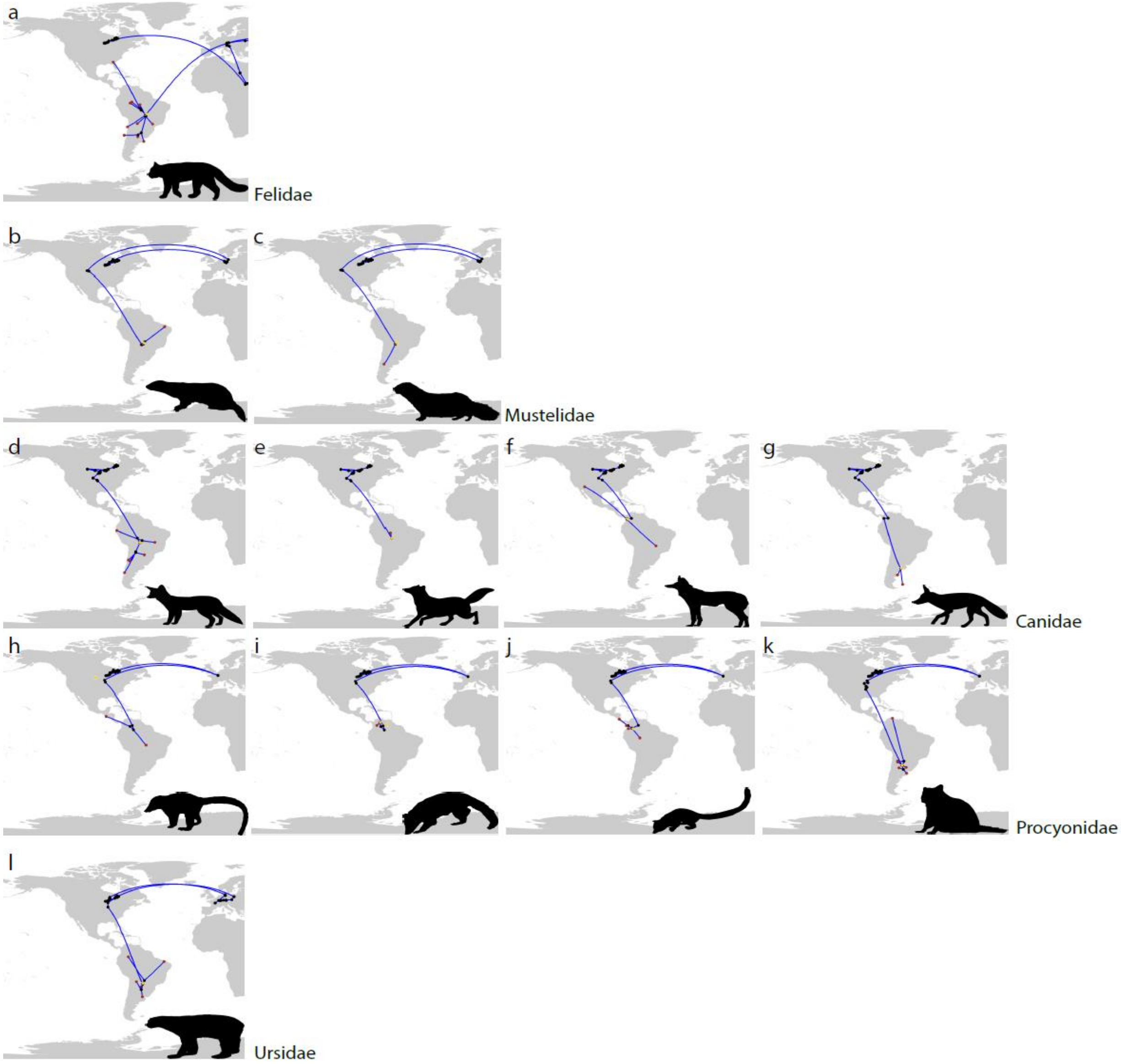


Figure 7. Center of origin and "Root to tip" geographic paths of the South American endemic genera. Black dots are nodes between ancestors of South American lineages; the yellow star is the median value of the estimated location of the ancestor of each South American genera; Red dots are tips of the South American genera. South American genera are a) *Leopardus* (Felidae); b) *Galictis* and c) *Lyncodon* (Mustelidae); d) *Lycalopex,* e) *Atelocynus,* f) *Chrysocyon,* and g) *Dusicyon* (Canidae); h) *Nasua*, i) *Nasuella*, j) *Bassaricyon,* and k) *Cyonasua*-group† (Procyonidae); l) *Arctotherium*† (Ursidae). Black silhouettes of species were obtained from PhyloPic.

DISCUSSION

We reconstructed the ancestral locations of the mammalian carnivores in the phylogenetic tree to fill the gaps in the fossil record and uncover the carnivore's paths across the globe, including the colonization events toward different landmasses. This allowed us to understand the biogeographic history of both the extinct and extant diversity under a new approach that considers the most realistic nature of the geography and the biogeographic processes until now. Our results based on the complete phylogeny and the geographic location of both extant and extinct diversity stand out North America as an important center of origin of early lineages, as the complete clade of mammalian carnivores, and the Oxyaenidae† and Carnivoramorpha groups. These results were consistent between the complete phylogeny, i.e., considering all groups as part of a monophyletic group, and when both clades were considered as independent monophyletic groups without an MCRA between them. On the other hand, the origin of the Hyaenodonta† clade is in Europe. Also, the most common recent common ancestor for

Carnivoramorpha and Hyaenodonta was dated from the Late Cretaceous, being older than previously reported. Our study offers a comprehensive biogeographical account of Carnivoramorpha, shedding light on the current diversity of mammalian carnivores, with a focus on South America as their most recent continental expansion.

About the early clades

Oxyaenidae†

Our results consistently show that Oxyaenidae† originated in North America during the Late Paleocene around 60 mya. Specifically, during Tiffanian North American Stage [the geologic timescale according to the North American Land Mammal Ages chronology (NALMA)]. Results are consistent with previous common assumptions based on the fossil record about the center of origin and most diversification in North America (Gingerich 1980; Gunnell 1998; Chester et al. 2010; Friscia & Van Valkenburgh 2010; Solé et al. 2011). Two fast, independent dispersal events, probably via Arctic Canada and Greenland (McKenna 1975; Eberle & McKenna 2002), allowed oxyaenids to arrive in Europe right after the Paleocene/Eocene transition (55 mya), and they went extinct rapidly there. Similarly, a unique fast long-distance dispersal was estimated toward Asia (Granger 1938; Smith & Smith 2001; Solé et al. 2011). These dispersal events are part of the recognized faunal interchange of the Paleocene-Eocene Thermal Maximum (PETM) (Mammalian Dispersal Event (Smith & Smith 2001, 2010; Solé et al. 2011, 2013b, 2014a; Eberle & Greenwood 2012) and probably dispersed through the De Geer route because they are known in Ellesmere islands (Eberle & McKenna 2002; Eberle & Greenwood 2012).

Hyaenodonta†

In the first instance, our results differed depending on whether we treated Hyaenodonta† as a separate group or as an early divergent subclade of the largest group of carnivore mammals, as considered in Faurby et al. (2019). Whatever the case, according to this phylogeny, the group is older (around 77 mya) than recently reported, for example, by Borth et al. (2019), where authors say the group originated in the Early Paleocene (65 mya). Finally, we estimate a European origin that agrees with the most recent proposals (Borths et al. 2016; Borth & Stevens 2019). In these works, separate biogeographic methods (parsimony optimization, likelihood optimization, Bayesian Binary MCMC, RASP) were applied to ancestral state reconstruction using four designated continental areas (Afro-Arabia, Asia, Europe, and North America). Related to the discrepancy, the geographical origin of Hyaenodonta† has been proposed as problematic due that the putative explosive radiation of the group is not fully captured in the fossil record. Unlike North America, the Paleocene of Europe is still not well sampled (Borths et al. 2016). Even studies suggesting a non-North American origin for this clade have proposed an extremely rapid dispersal to and substantial diversification within North America (Borths et al. 2016; Solé et al. 2016; Faurby et al. 2019), which can lead to misleading estimates. The highest speeds of movement that we estimated are found between the lineages that disperse between North America and Eurasia, reinforcing this previous idea based on the fossil record of fast dispersals between northern landmasses (Hooker 1996, 1998; Smith & Smith 2001, 2010; Solé et al. 2011). However, this discrepancy between our results seems biased to a North American origin by the position of the Hyaenodonta clade within the mammalian carnivore's phylogeny and the position of the north american basal *Altacreodus magnus* species. In Faurby's phylogeny (2019), Oxyaenidae† and Hyaenodonta† are sister clades (Creodonta) with *A. magnus* as the steam position of the crown Hyaenodonta. Previously the position of this species has been proposed as an outgroup in phylogenetical reconstructions of Hyaenodonta systematic (Borths et al. 2019; Solé et al. 2020). Hyaenodonta† was the first group to colonize Africa, and our results show that there were nine independent events since 71 mya (Late Cretaceous). Eight transition events towards Africa occurred in the Hyainailouroidea† superfamily since 52 mya (Early Eocene), whose origin was in Europe in contrast to results by Borths & Stevens (2019) that found an African origin. Nevertheless, their three subfamilies: Hyainailourinae†, Apterodontinae†, and Teratondontinae† have an African origin. Mattingly et al. (2020) mentioned that the early presence of the hyainailouroids in Africa indicates greater faunal connectivity between Eurasia and Africa during the Eocene than expected. Wetter climatic conditions of the Eocene would have been far more conducive for sweepstakes dispersal (e.g., rafting) across the Tethyan marine barrier (Gheerbrant & Rage 2006; Beard 2016). On the other hand, our results show a North American origin for the Limnocyoninae† subfamily resolving the uncertainty found by Borths & Stevens (2019), and a European origin for Proviverrinae† and Hyaenodontinae†, supporting the center of origin proposed for the first and contrasting for the second due the previous

Asian proposal (Borths & Stevens 2019). Discrepancies in some centers of origin are due to the different topologies recovered between the phylogeny used here (Faurby et al. 2019) and the previous systematic studies for the group (Borths et al. 2016; Borths & Seiffert 2017; Borths & Stevens 2019). Particularly for the Hyaenodonta† clade, although the internal lineages of the phylogeny were constrained according to previous works, the position of some sister clades differs from previous systematic proposals and, therefore, the subsequent ancestral biogeographic inferences. Hyaenodonta† was the group that showed the higher uncertainty in our estimations of the center of origin and biogeographic history.

Carnivoramorpha

Our results show unequivocally that the center of origin of Carnivoramorpha is in North America during the Late Cretaceous around 77 mya. We obtained the same result for Hyaenodonta†, considered an internal clade of carnivore mammals, specifically during Judithian NALMA. This era may represent the peak of dinosaur evolution in North America (Lehman 2001). Also, the center of origin of the extinct Viverravidae† family and Carnivoraformes (crown group Carnivora + the stem family Miacidae†; Flynn et al. 2010) has been estimated in North America during the Late Cretaceous (70 and 67 mya, respectively) that corresponds to Judithian NALMA, but both groups were importantly diversified in the Paleocene and Eocene (Flynn 1998; Qiu & Li 1977; Huang & Zheng 2005; Tong & Wang 2006; Solé & Smith 2013). Regarding Viverravidae†, our results agree with Solé & Smith (2013), who hypothesized that North America seems to be the most probable center of origin for viverravids compared to Asia due to their important radiation in the continent, which was inferred from the fossil record. The Viverravidae† is mostly known in North America, where they have been well-diversified since the Torrejonian (Early Paleocene) (Gingerich & Winkler 1985; Polly 1997; Meehan & Wilson 2002). Also, our results show only one dispersal event to Asia 63 mya (Early Paleocene), probably for the few connections through Bering land bridges that allowed few mammals to disperse (Beard 1998; Missiaen 2011). This occurred before a short period of global warming that favored the large-scale faunal exchanges: the Mammal Dispersal Event (MDE) in the Paleocene-Eocene Thermal Maximum (PETM) (Manchester 1999; Eberle & Greenwood 2012; Solé & Smith 2013). Regarding Carnivoraformes (Miacidae† family + Carnivora order), our results show an origin in North America 67 mya (Late Cretaceous) corresponding to Judithian NALMA, contrarily to an Asian origin proposed based on the observed biochronological and geographic distributions of the fossil record (Solé & Smith 2013; Solé et al. 2016). However, these studies mention that "one must keep in mind that a European or North American origin for the carnivoraforms cannot be completely dismissed", mainly due to the phylogenetic uncertainty at the base of the early evolution of the group, i.e., Miacidae† family. In the phylogeny used here, only Miacidae† and Stenoplesictidae† families were not constrained to be monophyletic. Therefore, the authors included all species in the backbone phylogeny constructed based on morphological data for extinct species (Faurby et al. 2019). For Miacidae†, our results show five independent dispersal events from North America to Eurasia between 55 to 40 mya averaging 6,400 km traveled and related to the PETM. Among the carnivoraformes, only miacids are involved in these dispersals (Solé & Smith 2013).

Carnivora order: a history not truncated towards the present.

Our results show that the crown Carnivora order has a North American origin 47 mya (Middle Eocene) during the Bridgerian NALMA. This result contrasts with the proposal of an origin in Central Asia based on the ancestral area reconstruction of extant species, excluding, for example, the basal Nimravidae† and Stenoplecticidae† extinct families (Rolland et al. 2015). Nevertheless, this idea was previously mentioned by Friscia & Van Valkenburgh (2010) based on fossil records. In the same way, the center of origin for early divergent suborders Feliformia and Caniformia is on the same continent. Feliformia suborder originated in North America 46 mya (Middle Eocene) as the basal Nimravidae† and the paraphyletic Stenoplecticidae† extinct families (34 and 45 mya, respectively). There has previously been proposed an uncertain center of origin between North America and Asia for Nimravidae† (Barycka 2006; Barret et al. 2021). Thus, for Nimravidae† and Stenoplecticidae† families, our results show that, from North America, six dispersal events to Europe and one to Asia since 34 mya (Late Eocene) occurred, allowing their wide distribution across Laurasia until their extinction six mya. Then, the MRCA for all extant feliform families shows an origin in Africa 41 mya (Middle Eocene), being one of the longest-distance dispersal estimated (10,493 kilometers) due to the lack of intermediate steps in the geographical connection between North America and Africa. That is an unclear biogeographical path to resolve in future works. Recent studies based on only molecular data suggest a potential Oligocene presence of Carnivora in Africa and that their arrival corresponds to the closure of the Tethys Sea (Yoder et al. 2003; Eizirik et al. 2010; Rolland et al. 2015). However, our results show the presence of Carnivora (at least Feliformia) in Africa data since 10 million years before this closure. Biogeographically, the Eocene presence of a feliform ancestor in Africa implies that the lineage must have colonized the continent by rafting rather than dispersal across a land bridge, because the tectonic collision between Africa and Eurasia did not occur until sometime near the Oligocene-Miocene boundary (Kappelman et al. 2003; McQuarrie & van Hinsbergen, 2013; Torfstein & Steinberg 2020). The same scenario was suggested for hyainailouroids† (see above). Nandiniidae family shows an African origin of 38 mya, agreeing with previous works based on molecular data and the current distribution of both family species (Rolland et al. 2015; Zhou et al. 2017). An African lineage traveled about 6,000 km to south Asia 19 mya (Early Miocene), where the Prionodontidae family originated seven mya (Late Miocene). Probably this route was via the Arabian microplate (Gaubert & Cordeiro-Estrela 2006; Wang et al. 2013). Other African lineage traveled nearly 2,700 km to Europe 31 mya (Early Oligocene) giving rise to the Barbourofelidae† + Felidae families' common ancestor. Then, a direct descendant lineage of this European ancestor dispersed back to Africa, giving rise to Barbourofelidae† 21 mya (Early Miocene). Our results also support the previous ideas of an African origin of barbourofelids based on fossil record (Barycka 2006), but a recent proposal changed their phylogenetical position (as an ingroup of Nimravidae†). This recent proposal showed an origin in Europe (Barrett et al. 2021). Pires et al. (2015) proposed a Eurasian origin based on the fossil record. Two dispersal events towards Europe were estimated since 19 mya and three towards North America from Europe since 13 mya.

Regarding Felidae, our results show a European origin 29 mya (Middle Eocene), which agrees with Pires et al. (2015) results inferred from the fossil record, which also contrasts the previous proposals of an Asian origin (Johnson et al. 2006; Zhou et al. 2017), or an uncertain origin (Rolland et a. 2015), all based on molecular data of extant species. In this study, using fossil and extant species, we included 69 extinct species, most of which are part of the stem diversity of the 43 extant felids species. Thus, a European ancestor dispersed to Asia 20 mya (Early Miocene), where the ancestor of extant diversity originated 14 mya (Middle Miocene), including Pantherinae and Felinae subfamilies. This last result agrees with Tseng et al. (2014). The colonization of Africa started from a European ancestor, 21 mya. Then 14 dispersal events were estimated to Africa, probably via the Arabian Peninsula that closely approximated Eurasia since Late Oligocene, facilitating periodic faunal interchange between the African continent and Eurasia (Gheerbrant & Rage 2006; Seiffert 2012). Twelve dispersals towards North America were estimated since 24 mya. Also, Felidae is the unique feliform family to colonize South America with five independent events since 7 mya (Late Miocene). Viverridae + Eupleridae + Herpestidae + Percrocutidae† and + Hyaenidae families have a common African ancestor that lived 34 mya (Early Oligocene). Viverridae originated 28 mya (Middle Oligocene) from this African ancestor and dispersed towards Europe since 22 mya (Early Miocene). Then they distributed in all Laurasia, in contrast with the previous hypothesis of an origin in Asia (Morales et al. 2000; Gaubert & Cordeiro-Estrela 2006;

Nyakatura & Bininda-Emonds 2012; Zhou et al. 2017) or uncertain (Hunt 2001; Barycka2006; Rolland et al. 2015). The family Herpestidae originated in Africa 30 mya (Early Oligocene) to disperse four times towards Europe and two times towards Asia later, contrasting the previous proposal of an Asian origin (Morales et al. 2000). The Herpestids sister lineage dispersed to Madagascar, where the endemic Eupleridae family originated 17 mya (Early Miocene). Recently, there has been proposed that this colonization of Madagascar was associated with a second continuous or near-continuous land connection established between Africa and south-western Madagascar as a result of regional uplift associated with the formation of the East African Rift System (Wit 2003; Delaunay 2018; Masters et al. 2021). The ancestor of the Hyaenidae + Percrocutidae† families lived in Africa 31 mya (Early Oligocene), and from here, a lineage dispersed 1,840 kilometers to Europe where the Hyaenidae family originated 17 mya (Early Miocene). This result contrasts with the previous proposal of an African origin based on molecular data of extant species (Rolland et al. 2015; Zhou et al. 2017). However, the oldest hyaenids known are from Western Europe (Hunt & Solounias 1991; Werdelin & Solounias 1996; Barycka 2006). That is a clear example of inaccurate ancestral estimations when using extant information only, as the hyenids' extinct diversity is vastly more abundant and geographically spread than the extant diversity of four species distributed only in Africa (Werdelin & Solounias 1991; Barycka 2006, Tseng et al. 2016). Our results also show that eight dispersal events occurred towards Asia since 16 mya, towards Africa 15 mya (Early Miocene), and a unique and longest dispersal (9,417 km) presumably via the Beringian land bridge towards North America (Tseng et al. 2019) where *Chasmaporthetes ossifragus* originated 6 mya (Late Miocene). Percrocutidae† family shows an uncertain origin between South Europe and North Africa 17 mya (Early Miocene). Independent of their precise center of origin, a unique and the longest (6,053 kilometers) dispersal event was estimated toward Asia. Percrocutids reached a wide distribution in Eurasia and Africa until their extinction 3 mya (Pliocene). In summary, the phylogenetic relationship at the family level of feliforms, at least for the extant families, in the phylogeny here used agrees with the previous phylogenetic proposals (Flynn et al. 2005; Gaubert & Cordeiro-Estrela 2006; Koepfli et al. 2006; Zhou et al. 2017). Therefore, our contrasting results (i.e., Felidae, Viverridae, and Hyaenidae) with some previous center of origin proposals are mainly due to including of vast fossil records in our research.

On the other hand, the Caniformia suborder originated in North America 47 mya (Middle Eocene) during the Bridgerian NALMA. Our results contrast the Asian origin proposal based on the ancestral area reconstruction of extant species (Rolland et al. 2015). The first lineage to diverge is the North American basal *Lycophocyon hutchisoni*† (Tomiya 2011). The common ancestor of the Amphicyonidae† + Canidae families lived in North America 46 mya (Middle Eocene), the continent where both families originated, which agrees with proposals based on the fossil record (Hunt 2005; Pires et al. 2015). The extinct Amphicyonidae† family, commonly called the 'bear dogs', represents a major group of caniforms in North America from 44 mya (Late Eocene) to 9 mya (Late Miocene; Hunt 1998). Recently, based on fossil specimens and their inclusion in a cladistic analysis, Tomiya & Tsend (2016) said that the amphichyonids' precise geographical origin remains uncertain. However, it is plausible that southern North America was an important stage for a very early phase of amphicyonid radiation. For amphicyonids, six dispersals towards Europe since 38 mya (Middle Eocene) were estimated. From Europe, six dispersals towards Asia since 25 mya, and six towards Africa since 23 mya (Late Oligocene). A unique and long (12,116 kilometers) dispersal from North America to Asia 38 mya (Middle Eocene). The Canidae family originated in North America 44 mya (Middle Eocene), supporting the previous findings (Wang & Tedford 2008; Prothero 2013; Pires et al. 2015). Within Canidae, successive radiations gave rise to three subfamilies by the end of the Oligocene: Hesperocyoninae†, Borophaginae†, and Caninae. The first two are now extinct and were restricted to North America. At the same time, Caninae radiated over almost the entire planet allowed by two geological events when lineages were able to reach Eurasia and South America around 15 million years ago (Geffen et al. 1996; Wang & Tedford 2008; Potter & Szatmari 2009; Porto et al. 2023). Ten colonization events in Africa were estimated since 12 mya (Middle Miocene), and five of these were from North America, on average the longest estimated for the family (10,288 kilometers). Also, 20 dispersals between North America and Eurasia since 11 mya (Middle Miocene), and six dispersals towards South America since 7 mya (Late Miocene) were estimated. The Arctoidea clade (Ursidae + Ailuridae + Mephitidae + Procyonidae + Mustelidae families) diverged from a North American common ancestor that lived 42 mya (Middle Eocene). The Ursidae family originated 41 mya in North America, agreeing with previous findings based on the fossil record (Hunt 2005; Goswami & Friscia 2010; Pires et al. 2015). Five dispersals to Eurasia between 39-32 mya (Late Eocene – Early Oligocene) occurred soon after their origin. *Agriotherium africanum* is the unique extinct ursid reported in Africa (except for the subspecies *Ursus arctos crowtheri*) and arrived 8 mya (Late Miocene) from Europe. Two dispersals towards South America were estimated: The ancestor of the genus *Arctotherium* 7 mya (Late Miocene) and the species *Tremarctos ornatus* 1 mya (Pleistocene). Our results show an origin in North America 37 mya (Late Eocene) for the Musteloidea group (Ailuridae + Mephitidae + Procyonidae + Mustelidae families), the sister clade of the Ursidae family. Two competing hypotheses are based on extant diversity regarding the center of origin for the crown clade Musteloidea. One proposes Asia (Sato et al. 2009; Sato et al. 2012), whereas the other favors North America (Yonezawa et al. 2007). Our biogeographic results strongly support the second hypothesis. Whitin Musteloidea, the family Ailuridae originated from a North American ancestor that dispersed to Europe 29 mya (Middle Oligocene). Our analysis which includes 12 extinct species agrees with previous proposals based on the fossil record (Janis 1998; Peigné et al. 2005; Salesa et al. 2022) and disagrees with results based on the Asiatic distribution of the unique extant specie *Ailurus fulgens* (Rolland et al. 2015). Two European ailurid lineages dispersed back to North America at 20 and 7 mya. Both events are the longest estimated for the family averaging 8,570 km. Also, two dispersals towards Asia were estimated at 6 mya. Similarly, for the ailurids, our results show that the family Mephitidae originated in Europe from an ancestor coming from North America 36 mya (Late Eocene). This result agrees with previous proposals based on the fossil record (Wang & Qiu 2004; Pires et al. 2015; Koepfli et al. 2017) and disagrees with an uncertain origin based on extant diversity (Rolland et al. 2015). The arrival of mephitids to North America resulted from the single invasion of a lineage that dispersed 7,550 km 20 mya (Early Miocene) across the Bering Land Bridge (Wang et al. 2005b; Koepfli et al. 2017). Then, a North American lineage of the genus *Conepatus* colonized South America 3 mya (Pliocene) in a dispersal of 7,825 km. Like Ailuridae and Mephitidae families, the Procyonidae family originates in Europe 31 mya (Middle Oligocene) from a North American ancestor that dispersed 5,688 km. Fossils indicate that the first procyonids originated in Western Eurasia (Wolsan 1993; Wolsan & Lange-Badré 1996; Pires et al. 2015; Koepfli et al. 2017), and ancestral reconstructions based on extant diversity show an origin in North America (Rolland et al. 2015). According to the fossil record, procyonids did not arrive in North America until the Early Miocene (Hunt 1996; Baskin 1998, 2004; Koepfli et al. 2017). However, our results show that the unique dispersal to North America was 31 mya (Middle Oligocene). Procyonidae was the first family to arrive in South America, and our results show five independent dispersal events (These results are discussed detailed in the next section). Our results show an origin in North America for the Mustelidae family 28 mya, and their first dispersals to Eurasia started at 26 mya (Late Oligocene), which agrees with Pires et al. 2015. The biogeographic origin of Mustelidae is considered by many as Eurasian (Tedford et al. 1987, 2004; Baskin 1998; Koepfli et al. 2008; Sato et al. 2012). Thus their record in North America is interpreted as the result of repeated or episodic invasions from Asiatic or European taxa via Beringea or Artic Canadian islands, respectively. However, an equally likely North American or European biogeographic scenario for such origin has been convincingly argued by Wang et al. 2005b and Ferrusquía-Villafranca et al. 2021. The conflict is that the geographic distribution of some European fossils (e.g., *Plesictis* and *Mustelictis*) suggests that the early evolution of

Mustelidae took place in Europe, but the direct ancestor is North American. In this sense, our results show that the direct descendant from the Arctoidea ancestor or even from the Caniformia ancestor to the Mustelidae ancestor was always in North America. Furthermore, although the first dispersal event was from North America to Europe (five dispersals since 26 mya were estimated), the number of events from Europe to North America is much higher (22 dispersals since 21 mya were estimated). Three dispersals were estimated from North America towards Asia since 19 mya and two bi-directional dispersals since 2 mya. All these dispersals suggest that mustelids moved across Beringia and Artic Canadian in both ways during different intervals when the land bridge between Eurasia and North America was open (Koepfli et al. 2008). Six dispersals towards Africa since 14 mya and five towards South America were estimated.

South America: the most recent history.

It is striking that most carnivore lineages that colonized South America belong to the several families of the Caniformia suborder (Canidae, Mephitidae, Mustelidae, Procyonidae, and Ursidae) while only one family of the Feliformia suborder (Felidae) arrived at South America. Although both suborders originated in North America, the ancient feliform moved early to Eurasia, and the MCRA for all extant families shows an origin in Africa. At the same time, while the caniforms stayed mainly in North America, geographically close to the South, which allowed their migration to South America when the geological conditions were optimal. Historically, studies of the fossil record have postulated that the first Carnivora lineage that arrived in South America was the procyonid ancestor of the endemic *Cyonasua*-group† 9 mya (genera *Cyonasua*† and *Chapalmalania*†; Reguero & Candela 2001; Prevosti et al. 2012; Prevosti et al. 2013; Forasiepi et al. 2014). *Cyonasua*-group† is thought to have dispersed into South America via island hopping or rafting during the Late Miocene (Simpson's waif dispersal) when the inter-American seaway consisted of a large archipelago during a time when global sea level was relatively low (Haq et al. 1987; Coates & Obando 1996; Miller et al. 2005). Our results show that *Cyonasua-group* started its dispersal from North America 13 mya, and their center of origin was in Southern South America 9 mya (Figure 8k) after moving 8,051 km before the Great American Biotic Interchange (GABI). This result agrees with previous studies (Patterson & Pascual 1972; Prevosti et al. 2013; Pino et al. 2022). Interpretations of the fossil record say that procyonids immigrated twice to South America, in the Late Miocene to give rise to *Cyonasua*-group†, and again in the Late Pleistocene for the living taxa, which is inconsistent with phylogenetic reconstructions that indicate multiple immigration events (Prevosti et al. 2012). In this sense, our results show that other procyonid lineage arrived in South America even before *Cyonasua-group*†. The MCRA of *Bassaricyon* + *Nasua* + *Nasuella* genera show an origin in northern South America 16 mya, after a journey of 4,720 km from North America (Figure 8h-j). Thus, our results disagree with classical proposals of the arrival of non-*Cyonasua* procyonids to South America for a recent second time with other mammalian taxa as part of the "legions of the north" during the GABI ca. 2–3mya (Simpson 1980; Marshall 1988; Marshall et al. 1982; Webb 1985). Nevertheless, our results agree with the seminal idea based on molecular data of Koepfli et al. (2007) and recently supported by Ruíz-García et al. (2022) that suggest that these taxa may have entered South America at the same time as *Cyonasua*-group† also via island hopping. Two additional dispersal events towards South America have been estimated within the Procyonidae family during the Miocene-Pliocene: *Procyon cancrivorus* and *Potos flavus*. Within Canidae, our results show six independent events of colonization of South America since 10 mya (Middle Miocene), which agree with the paleontological perspective of several waves of migration (Prevosti 2010; Eizirik 2012; Prevosti et al. 2012; Moura Bubadué et al. 2016; Prevosti & Forasiepi 2018). However, these results disagree with recent proposals based on molecular data that propose only one colonization event, which then diversified in the extinct and extant diversity of South American canids (Chavez et al. 2022; Porto et al. 2023). In this sense, Porto et al. (2023) found a unique event around 10 mya based on the ancestral area reconstructions of extant and extinct diversity, and Chavez et al. (2022) found a unique event of 3.9-35 mya based on genomic data of the extant species. The difference between these and our results is the consideration of certain North American fossils. For example, Chavez et al. (2023) do not consider some fossil remains from the Early Pliocene, ~5 mya (predate the closure of the Panamanian land bridge), and their use could be conclusive evidence against a single dispersal model. Our results show that the center of origin of the genus *Chrysocyon* is in Northern South America, of the *Lycalopex, Protocyon, Cerdocyon,* and *Atelocynus* genera is in Central South America, and of *Dusicyon*† is in Southern South America (Figure 8d-g). All these estimated centers of origin agree with the results of Chavez et al. (2022) of an origin in the Eastern Andes. Within Ursidae, our results show two independent events of colonization of South America between 1.1 and 0.8 mya

(Pleistocene), which agree with the paleontological perspective (Hunt 1996; Flynn & Wesley-Hunt 2005; Prevosti et al. 2012). After the GABI, during the Late Pliocene or Early Pleistocene, one migration of North American bears give rise to South American *Arctotherium*† and a second immigration event should have given rise to *Tremarctos* in South America (Soibelzon & Prevosti 2013). Our results disagree with the hypothesis proposed by two recent works that mention *Tremarctos* may not have arrived in South America in a second and independent immigration event. In contrast, it originated in situ from a common ancestor with *Arctotherium*† in South America. This should mean that *Tremarctos*, or the ancestor of *Tremarctos*, could have lived in South America much earlier than traditionally thought. Authors say that the non-existence of fossils older than 7,000 years does not necessarily imply that the Andean bear cannot be older (Mitchell et al. 2016; Ruíz-García et al. 2020). Also, our results show that the center of origin of South American *Arctotherium*† is in Central South America. Within Mustelidae, our results show five independent colonization events towards South America that diversified in the extant local genera and species. This result agrees with the classical view based on the fossil record postulating that all these dispersals were part of the GABI, following the rise of the Panamanian isthmus, 3-2.5 mya (Marshall & Sempere 1993; Coates & Obando 1996; Hunt 1996). Our results, like those obtained by Koepfli et al. 2008, show that two of five South American colonization events come from Europe: *Eira barbara* and *Pteronura brasiliensis* species, being the longest dispersals (9400 kilometers on average) estimated for the family. These results are anomalous because these mustelid genera have been related to extinct taxa from North America, suggesting a more proximate origin for these lineages (Bjork 1970; Ray et al. 1981). However, paleontological studies suggest that the ultimate ancestry of these extinct taxa lies in Europe (Ray et al. 1981; Willemsen 1992; Koepfli et al. 2008). That may probably be due to the lack of intermediate fossils in the geographical path (phylogenetic branch) between Europe and South America or due to their ancestors' effective long-dispersal events, as estimated here. The ancestor of both South American *Mustela* (*Mustela felipei* and *Mustela africana*) arrived 2.4 mya from North America after the Panamanian isthmus was in place, agreeing with previous proposals based on fossil record (Marshall et al. 1984; Hunt 1996). Similarly, the ancestor of South American *Lontra* (*Lontra felina* + *Lontra provocax* + *Lontra longicaudis*) arrived at 1.9 mya, agreeing with previous proposals based on fossil records (Koepfli et al. 2008). Also, our results show that *Lyncodon* + *Prepoecilogale*† + *Galictis* genera have an MCRA that arrives in South America 4.2 mya (Pliocene) and that the center of origin of the endemic *Galictis* and *Lyncodon* genera is in Central South America. Within Mephitidae, our results show only one dispersal event of a North American ancestor that arrived 1.4 mya (Pleistocene) to Central South America has diversified in the three South American *Conepatus* species (*Conepatus chinga* + *Conepatus humboldtii* + *Conepatus semistriatus*). These results agree with previous proposals based on fossil records (Baskin 1998; Wang & Carranza-Castañeda 2008; Prevosti et al. 2012; Prevosti & Forasiepi 2018). Finally, within the Feliformia suborder, the family Felidae is the only one that arrived in South America from five dispersal events since 7 mya (Late Miocene). They represent three subfamilies: Felinae, Pantherinae (“conical-toothed” cats), and the extinct Machairodontinae† (“saber-toothed” cats). Two dispersal events (*Panthera onca* and the

MCRA of genus *Leopardus*) were estimated from Europe to South America (like *Pteronura* and *Eira* cases in the Mustelidae family; see above), being part of the longest (11,700 km on average) and fastest (6,300 km/myr on average) distances estimated, probably due to the lack of intermediate geographical steps between Europe and South America. In this sense, Johnson et al. (2006) mentioned that after the split with the *Panthera* ancestor in Europe, the ancestor of the current jaguar rapidly colonized South America. Our results show that the center of origin of the genus *Leopardus* is in Central South America, with posterior dispersal and diversification to the rest of the continent. Also, our results show that the genus *Puma* arrived in South America in two independent events, *Puma yagouaroundi* 7 mya (Late Miocene) and *Puma concolor* 4 mya (Early Pliocene), which agrees with previous works postulating that these species diverged presumably in North or Central America and the ancestor of the current jaguarundi migrated South America more rapidly than the ancestor of the puma (Johnson et al. 2006; Ruíz-García et al. 2022). However, our results disagree with recent proposals of a unique dispersal (Chimento & Dondas 2018). Although the event would suggest that modern pumas originated from a North American ancestry, the puma fossil record in South America is so poor that a more recent neotropical origin and northward dispersal cannot be ruled out (Kurten 1976; Werdelin 1989; Chimento & Dondas 2018). Finally, our results show that *Smilodon populator*† arrived in South America at 0.7 mya in agreement with previous proposals (Berta 1985; Kurten & Werdelin, 1990; Cione & Tonni 2005; Prevosti et al. 2006)

CONCLUSIONS

Recent advancements in biodiversity research, including more detailed knowledge of phylogenetic relationships and geographic distribution through accessible methodologies, have allowed for a more accurate understanding of natural history and the ability to reinterpret previously known patterns and processes. Through these new approaches, we have discovered that North America played a significant role in the origin of early terrestrial mammalian carnivores, except for Hyaenodonta, which originated in Europe. Results of the Ailuridae, Mustelidae, Hyaenidae, Felidae, and Viverridae families confirm the notion that the current diversity does not allow estimate accurate centers of origin due to the lack of vast extinct diversity, and at the same time, the results of early groups such as Hyaenodonta, Carnivora, Caniformia, and Feliformia confirm the notion that fossil diversity needs a clear phylogenetic position to estimate an accuracy center of origin. Our research has provided a comprehensive biogeographical history of Carnivoramorpha, including various extinct species and trans-continental dispersals that explain the present distribution of Carnivora. Additionally, our findings have enabled the quantification of endemic lineages and their place and time of origin in different continents, as demonstrated in our study of South America.

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CHAPTER 2: How to survive on the journey: Fast body size evolution associated with long geographic dispersal in mammalian carnivores.

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ABSTRACT

The evolution and origin of biodiversity have long been attributed to the macro-scale biogeographical process of dispersal ability. However, obtaining accurate measurements of this process has historically been a challenge. To address this, we utilized the Geomodel to estimate the travel distances of each species of terrestrial mammalian carnivores and identify whether they were intra-continental or trans-continental migrants. This allowed us to evaluate the "positive dispersal-evolution" and "Simpson's filter-bridge" hypotheses and investigate if this biogeographical process leads to fast evolution in body size due to environmental pressures. Our findings provide the first comprehensive assessment of dispersal ability across the mammalian carnivore phylogeny. For this, we also estimate the body mass evolution rate of the group. Our results show that dispersal ability is related positively to mammalian carnivores' body mass evolutionary rate, supporting thus the "positive dispersal-evolution". Thus, the estimated long-distance dispersal (LDD) explains the fast evolutionary change in several independent and mainly recent lineages of terrestrial mammalian carnivores and their highly discrepant body sizes. Our study indicates that the rapid changes in body mass resulting from LDDs can occur within the same "migrant" lineage or branch, supporting a filter effect. Additionally, in specific descendant clades, LDDs may serve as a facilitating event for the evolution of new clades upon arrival in a distant geographic area. In these cases, the journey represents an ecological opportunity preceding an adaptive process.

INTRODUCTION

Dispersal ability

Macro-scale biogeographic processes have been proposed in several classical hypotheses to explain the evolution and origin of biodiversity (Carlquist 1972; Cowie & Holland 2006; Crisp et al. 2011; Wiens & Donoghe 2004; Gillespie et al. 2012; Rodriguez-Silva & Schlupp 2021). For instance, species dispersal ability is a macro-scale biogeographical process postulated as the main factor explaining how far lineages can move away from their center of origin and consequently explains how much lineages can evolve (Altwegg et al. 2000; Clobert et al. 2001; Kokko & Lopez-Sepulcre 2006; Ronce 2007; Saastamoinen & Hanski 2008; O'donovan et al. 2018). This link between dispersal ability and evolution determines how many geographically distanced environments lineages can explore (Lomolino et al. 2006), propitiating even the colonization of new continents across great spatial and temporal scales. In this sense, the evolutionary forces play different roles in species with different dispersal abilities (Muller-Landau et al. 2003;

Crisp et al. 2011). Species with long-distance dispersal (LDD) ability could experience important phenotypical evolutionary shifts resulting in an acceleration of the evolutionary process due to the major changes in environmental conditions during the journey (Clark et al. 1998; Higgins et al. 2003; Viana et al. 2013). Additionally, high dispersal ability may facilitate the crossing of barriers and allow species to reach remote areas such as islands or continents where they could adapt to the new ecological opportunities (Lomolino et al. 2006).

On the other hand, the colonization of new continents, at least in terrestrial animals, has been postulated to be dependent on both the geographical and the temporal position of the natural barriers, bridges, or corridors between the landmasses, and the amount of variation in ecological traits within species which are also involved in the possibility to overcome the selective pressures exerted by the environment during the journey (Ricklefs 1987; Schooley & Wiens 2003). This last notion about trans-continental dispersal across terrestrial bridges under strong environmental pressures is the classic Simpson's filter-bridge hypothesis which brings an additional view about the relationship between dispersal distance and phenotypic evolution (Simpson 1940). Due to the challenging nature of quantifying species movement and dispersal ability, the two main hypotheses regarding species dispersal ability and phenotypic evolution have yet to be evaluated in large groups. Additionally, estimating LDDs at the species level has historically been difficult. Furthermore, evaluating these hypotheses in the deep past has proven challenging due to the rarity of events over large spatial scales and multiple generations

(Trakhtenbrot et al. 2005; Kokko & López-Sepulcre 2006; Lenoir et al. 2012; Stevens et al. 2014).

To delve further into the thesis chapter and provide a comprehensive understating, we will now elaborate on the two hypotheses that will be tested. The first is "The positive distance-evolution" and the second is "Simpson's filter-bridge" hypothesis. The “positive distance-evolution” hypothesis proposes that lineage's phenotypic evolution could go hand in hand with the "distance traveled" (LDD) during a long geographical movement, as the environments can be more different as species move further. Various environmental factors, including photoperiod, temperature, and water availability, influence the activity of vertebrates. These variables can either restrict or increase how much time animals can move efficiently. Therefore, moving further in space may only be possible due to quick ecomorphological evolution or the evolution of higher physiological tolerances that allow colonization of new environments. A positive relationship between dispersal ability and physiological changes associated with body mass has been found in mammals, reptiles, and amphibians (Hillman et al. 2014; Stevens et al. 2014). The "Simpson's filter-bridge" hypothesis suggests that the environment of a land bridge acts as a filter, allowing only certain species to cross between continents. Based on observations in the fossil record, this hypothesis implies that species distribution on each side of the bridge today or in the past reflects this selective process. In contrast to a corridor, a land bridge creates a unique environment that determines which species can successfully cross. For example, steppe plant species with trans-Beringian distributions were likely far more tolerant to climates of glacial intervals, including land-bridge environments (Edwards et al. 2018). Other taxa were unable to cross this bridge (Elias & Crocker 2008). In other words, the physical environment involved in the journey can limit the colonization event. However, the species' response to the selective pressure imposed by the bridge will depend on the phenotypic evolvability of migrant lineages. Thus, the availability of (1) a corridor without an environmental filter or a (2) filter-bridge means a geographical opportunity for lineages to colonize a particular new geographical space and, only under a filter bridge, is essential for species to possess the phenotypic capacity to respond quickly.

The phenotypic evolution

However, to evaluate this chapter's hypotheses, we also need to answer the question of what dispersal-related traits could respond at different rates, but this question has a more complex answer. This is because dispersal ability and dispersal distance are emergent properties (complex traits) resulting from the interactive effects of various dispersal-related traits (e.g., morphology, physiology, behavior, and life history traits), which are highly dependent on the type of organism studied (Ronce 2007; Bonte et al. 2012; Matthysen 2012; Ronce & Clobert 2012; Travis et al. 2012; Green et al. 2022; Alzate & Onstein 2022). Fortunately, animal body size is arguably the single-most important predictor of many aspects of the interactions between the environment and species dispersal ability (Peters 1983; LaBarbera 1989; Brown 1995; Bowman et al. 2002; Alzate & Onstein 2022), and it is possibly inferable from fossils. Therefore, the body size is one of the only traits that can be directly analyzed in both fossil and living species which in turn will allow testing of the study hypotheses, i.e., the relationship between dispersal ability and the rate of phenotypic evolution (Faurby et al. 2021). Previous works have postulated that the rate of body size evolution can accelerate under certain biogeographical process with changing conditions of temperature regimes (Cooper & Purvis 2010; Lawson & Weir 2014; Avaria-Llautureo et al. 2021) or the changing condition that generates the island effect (Lister 1989; Pergams & Ashley 1999; Clegg et al. 2002; Millien 2006). Such events of fast body size evolution represent, in several cases, evidence of positive phenotypic selection (Baker et al. 2015). Studies in *Anolis* lizards report variation in the rates of phenotypic evolution linked to ecological transitions to new habitats and environments, such as the colonization of new islands (Thomas & Freckleton 2012; Eastman et al. 2013). At the same time, these fast changes could go in a particular direction (i.e., increase or decrease the body size) and be associated with higher dispersal ability. Some examples are found in several taxa like insects (Roff 1991; Ness et al. 2004), fishes (Burns & Bloom 2020), birds (Hamilton 1961; Paradis et al. 1998), and mammals (Sutherland et al. 2000), where the positive relationship between body size and dispersal ability could be because bigger species are more efficient in term of consuming energy for long-distance dispersals (Burns & Bloom 2020). Consequently, it follows that transitions from one continent to another through a "filter-bridge" may be accompanied by rapid changes in body size. These could align with Simpson's well-known notion of quantum evolution (Simpson 1944; Kubo et al. 2018).

In terrestrial mammalian carnivores

For example, in mammalian carnivores, The De Geer, Thulean, and Beringia routes connected North America and Eurasia intermittently, and several times, allowing in the first instance the trans-continental dispersal of earlier lineages of Hayenodonta, Oxyanodonta, and Carnivoramorpha during Paleocene-Eocene (Beard 1998; Solé & Smith 2013; Brikiatis 2014). Then, several dispersal waves in the Late Neogene involved only Carnivoramorpha lineages (Qiu 2003). These dispersal events have been considered a climatically regulated pathway for biological dispersal and, therefore, a clear example of a "filter-bridge" (Sanmartín et al. 2001; Qiu 2003). Hyaenodonts were broadly distributed across Europe, North America, Asia, and Afro-Arabia during the Paleogene (Rose 2006) due to long dispersals between the continents (see results of the first chapter), and are a group that ranged in body mass from small weasel-sized species like North American *Thinocyon* (Gunnell 1998) and European *Eoproviverra* (Godinot 1981) to gigantic, rhinoceros-sized species like North American *Hemipsalodon* (Mellett 1969) and Afro-Arabian *Megistotherium* (Savage 1973). Previous works suggest that some mammalian carnivores that dispersed between North America and Eurasia during the faunal interchange of the Paleocene-Eocene Thermal Maximum (PETM; Smith & Smith 2001, 2010; Eberle & Greenwood 2012; Solé et al. 2021) decreased their body size (Gingerich 1989; Heinrich et al. 2008; Chester et al. 2010). There is also evidence for a decrease in the size of soil organisms during this interval (Smith et al. 2009). A recent work based only on fossil records found a positive relation between dispersal rates and body mass during the Beringian interchange of mammalian terrestrial carnivores (Hauffe et al. 2021). The dispersal and successful colonization of carnivores to the Kuril Islands in Asia appear to be functions of a body size "filtered" by the extreme climate in winter (Lomolino 1993; Hoekstra et al. 1998). Also, the formation of the Panama Isthmus that allowed the Great American Biotic Interchange (GABI) and the colonization of mammalian carnivores to South America has been proposed as a filter-bridge (Marshall 1988). Stehli & Webb (1985) suggested that this interchange began with a minor episode in which a few taxa crossed through a filter-bridge before the complete close of the terrestrial bridge. Then, a great wave of dispersal events occurred without problems when the isthmus became a corridor. During the interchange, recurrent glacial events and the sea level fluctuations that interrupted ground passage produced a filtering effect that determined which animals could disperse and when (Marshall 1988; Woodburne 2010; Prothero et al. 2014).

Our study aims to determine whether dispersal distance or the transition between continents is a better predictor of the rate of body mass evolution in mammalian carnivores. According to the "positive-distance evolution" hypothesis, long-distance dispersals (LDD) should lead to faster rates of body mass evolution due to greater environmental variation. Therefore, we predict that dispersal distance will have a positive effect on body mass evolutionary rate. Alternatively, the "Simpson's filter bridge" hypothesis suggests that lineages that transitioned between continents will exhibit higher rates of body size evolution than those that only dispersed within a single continent. However, these hypotheses are not mutually exclusive, as trans-continental dispersals may also be LDDs that contribute to rapid body mass evolution.

METHODS

Phylogeny

To get the geographical dispersal distance necessary to evaluate our two main hypotheses, a complete biogeographic framework regarding the place and time of origin for all ancestral species of mammalian carnivores is needed. Consequently, this research was conducted on a recent fossilized phylogeny of the group (Faurby et al. 2019). This phylogeny consists of a sample of 1,000 trees including 1,713 tips, both extinct and extant mammalian carnivores. Specifically, the phylogeny includes 198 extinct species of Hyaenodonta† and Oxyanidae† and 1,515 Carnivoramorpha species (Carnivoraformes + Viverravidae†). 314 species are extant and belong to the Carnivora order. This is the first species-level phylogeny of mammalian carnivores including all suitable fossils and all extant species. To infer the locations of all ancestral species, using the Geographical (Geo) model (see below), we used a Maximum Clade Credibility (MCC) tree constructed from the posterior sample trees. We modified 144 branches of fossil species with 0 lengths to run the Geomodel analysis. We assigned near-zero branch length (0.000001) to ensure that the Geomodel analysis will not modify the branch so that the estimated location fossil ancestral node is at the fossil location with high accuracy and precision (Avaria-Llautureo et al. 2021). Additionally, several species were removed from the phylogeny. First, *Miacis uintensis*, *Uintacyon major*, *Mustela larteti*, *Schlossericyon viverroides,* and *Stenogale aurelianensis* were removed because they were discovered to be junior synonyms (Faurby et al. 2021). Second, we removed one of the sister species when both had the same (duplicated) geographic coordinates. Third, we removed species without body size data (Pinnipedimorpha clade and other taxa), which is necessary for the posterior analysis of this chapter. Thus, the final phylogeny as input to Geomodel analysis contains 1,317 species (1040 extinct and 277 extant). Finally, due to the phylogenetic uncertainty raised in the relationship of the three early clades, we ran analyses using the complete phylogeny (1317 species) and for the three groups separately: Carnivoramorpha (1141 species), Hyaenodonta† (150 species), and Oxyaenidae† (26 species).

Geographic data

We obtained the geographic locations from different databases for each species, both extant and fossils in the phylogeny. For fossil species, we obtained the cartesian coordinates (longitude and latitude) mainly from the "Paleobiology Database" (PBDB; Peters & McClennen 2016). We downloaded and cleaned these fossil occurrence data using the “clean_fossils” function from the “CoordinateCleaner” R package. This function runs multiple empirical tests to identify occurrences with potentially erroneous coordinates and erroneous fossil ages (Zizka et al. 2019). Coordinates of fossil species absent in this database were obtained from specific literature, mainly from each fossil description paper. In these cases, we estimated the paleo coordinates from the present-day coordinates (fossil deposits) location based on the PALEOMAP model, which is implemented in the function "reconstruct" of the "choronosphere" R package (Kocsis & Raja 2020). For extant species, the neotropical records of Nagi-Reis et al. (2020) were preferred due to their updated compilation and systematization of records from different data sources. We obtained geographic coordinates from the GBIF database for the rest of the extant species. We used the protocol of Rolland et al. (2018) to download and clean the GBIF records. Finally, records for each extant species were overlapped with their respective distribution map available in IUCN red list to erase records outside the known distribution. Then, we applied several additional filters to data records before the definitive analyses. First, for sister species, we removed duplicated coordinates and those coordinates with a distance lower than 50 meters, as the Geomodel collapsed the branch lengths of sister carnivoran species to zero when they have duplicated coordinates or in a distance lower than 50 meters (given the phylogeny and data available in this study). Then, we obtained a random sample of 3,000 coordinates for species with more than 3,000 geographic records. This is because previous tests showed that more records do not improve the estimations and only delay the analysis. Finally, our dataset contained 120,694 records for the 1,317 phylogenetic tips. From this dataset, two input files for Geomodel analysis were generated, one that considers all the species in the phylogeny, i.e., species that have only one record (i.e., the centroid from the sample of coordinates or single occurrence data), and a second file that contains multiple records for species.

Dispersal estimations: intra or trans-continental dispersal distance traveled.

To evaluate the two main hypotheses, we obtained the dispersal abilities measured in the distance traveled (kilometers) for each mammalian carnivore's phylogeny lineage. For this, we estimated the paleo-distribution of ancestors in a continuous and three-dimensional space from the geographic locations within each species (both extant and fossils). Each phylogenetic node's ancestral locations were estimated using the Geomodel (O'Donovan et al. 2018) in the computer program BayesTraits 4.0 (Pagel et al. 2004). The model estimates the posterior distribution of ancestral locations measured in longitude and latitude while sampling across all location data within species and considering the spherical nature of Earth. These estimations are based on the variable-rates model (Venditti et al. 2011), which detects shifts away from a constant background rate of evolution in continuous traits (expected under BM) in whole clades or individual branches. For the Geomodel analyses, we ran four MCMC chains for 300,000,000 iterations, sampling every 50,000 iterations and discarding 250,000,000 as burn-in. The chain convergence was checked using the effective sample size (ESS) in Tracer v.1.7.1, ensuring outputs with ESS > 200. The final sample includes 1,000 posterior locations for each phylogenetic node. From the Geomodel outputs, we estimate the geographic distance historically dispersed for each lineage across each phylogenetic branch (branch-wise distances). Then these distances were summed along the path that links the root of the phylogenetic tree with the extant species (path-wise distances). The “branch-wise distances” were calculated using the “distCosine” function in the “geosphere” R package (Hijmans 2019). The distCosine function brings the shortest distance between two points, assuming a spherical Earth. To obtain the historical distance dispersed for each species and considering the uncertainty in ancestral locations estimates, the “branch-wise distances” for every one of the 1,000 locations estimated were calculated in the posterior sample and, therefore, 1,000 "path-wise distances" for each species in the phylogeny were obtained. Finally, given that each branch represents a dispersal event with a geographical distance estimated between its ancestral node and its descendant node, we identify and quantify the trans-continental and intra-continental dispersal events necessary for evaluating "Simpson's filter-bridge" hypothesis. For this, we categorize branches as follows: lineages (branches) whose posterior distribution of ancestral node was estimated in one continent and the posterior distribution of their descendant node was estimated in another continent corresponds to "migrant lineages", *i.e.*, experienced a trans-continental dispersal; and lineages whose posterior distribution of ancestral and descendant node was estimated in the same continent corresponding to "non-migrant lineages", i.e. experienced an intra-continental dispersal. Continents were categorized as North America, South America, Europe, Asia, Africa (including Arabian Peninsula + Madagascar), and Australia.

Body size data and the estimation of body size evolution rate

For body size data of fossil and extant tips, we downloaded the body mass values available in the recent CarniFOSS database (Faurby et al. 2021). This database contains the estimated body masses for all extant or fossil species within Hyaenodonta, Oxyaenodonta, and Carnivoramorpha, except for the monophyletic Pinnipedimorpha. Currently, there is no reliable body size estimates for fossil pinnipeds. Deriving a reasonable body size proxy that can be extrapolated to fossil taxa in this clade has proven difficult, as pinnipeds feed in different ways than terrestrial carnivorans and do not routinely support their body weight on their limbs (Finarelli & Flynn 2006). The body mass of several species was corrected from this database due to over- and underestimates produced by phylogenetic inferences alone (Faurby et al. 2021), for example, *Megistotherium osteothlastes* (Rasmussen et al. 1989). Finally, we obtained a body mass value for the 1,317 species in the phylogeny.

To study the body mass evolution, we compare two continuous traits evolution models: Brownian motion (BM; Felsenstein 1985; Pagel 1993) and Variable-rate (VR; Venditti et al. 2011), using a phylogenetic regression model where body mass is predicted by the time of phylogenetic tips and a quadratic term for time, i.e., Body mass $\sim \alpha + \beta_1(\text{Time}) + \beta_2(\text{Time}^2)$, due to the known relationship between these variables framed in the Cope's Rule: the tendency for organisms in evolving lineages to increase in size over time. This rule strongly holds for mammals (Jablonsky 1996; Alroy 1998; Kingsolver & Pfennig 2004; Hone & Benton 2004). The quadratic term is due to the curved shape of this relationship in our data. Including both predictors allows a better fit of the model and the stability of the “BM variance” parameter. If the BM model shows a better fit than VR, thus we reject both hypotheses because there are no differential rates in body size evolution throughout the evolutionary history of mammalian carnivores. When the VR is fitted to a single continuous trait, it estimates an underlying background BM rate of evolutionary change (σ^2_b); and a set of branch scalars, *r*, which define whether the trait is evolving faster (r>1) or slower (r< 1) than BM rate across each branch. The output then is a posterior distribution of phylogenetic trees with branch lengths scaled according to the amount of change that the trait of interest has accumulated across each branch. To summarize these rate shifts, we built a consensus tree out of the trees produced using the BayesTrees program. The best model, BM or VR, was selected by comparing the marginal likelihood calculated by the stepping-stone algorithm. When applied in a phylogenetic regression context, the Variable-rate model simultaneously estimates the background rate, the parameters of the regression, and the rate of evolution across phylogenetic branches. The difference is that in a regression context, the branch-wise rates of evolution are estimated to fit the residual variance of the regression, which is phylogenetically structured. In the case of VR showing a better fit, to obtain the amount of change accumulated by million years, i.e., the rate of body mass evolution, we divided the scaled branches by the branches of the time-calibrated tree.

Hypothesis 1: Simpson's filter-bridge.

We evaluate this hypothesis through two approaches. First, we tested directly if trans-continental dispersals are associated with faster evolution in body mass. For this, we compare the set of branches that represent trans-continental dispersals ("migrants") to the set that represents intra-continental dispersals ("non-migrants") using the Variable rate model with Branch-partition (Kubo et al. 2019). The Variable rate model with Branch-partition tests whether rates of body size evolution differ significantly across the partition of branches in the phylogenetic tree. This model allows us to explicitly evaluate the hypothesis in its structure [$\sigma^2_m > \sigma^2_b$, where σ^2_m is the rate of evolution associated with migrating branches, whereas σ^2_b is the background ("non-migrant") rate of evolution]. Branches were partitioned according to "migrants" or "non-migrants" lineages identified from Geomodel output. To identify the branch as migrants or non-migrants, we calculated the median value of the posterior probability of coordinates across every phylogenetic node. If the ancestral and descendant nodes across each branch were estimated in the same continent (e.g., ancestor=North America and descendant=North America), then we would assign that branch to a “non-migrant” partition. If they differed (e.g., ancestor=North America and descendant=South America), we would assign that branch to a “migrants” partition. We set the partitions using the local transform option for the VR model in BayesTraits. We ran four MCMC chains for 300,000,000 iterations, sampling every 50,000 iterations and discarding 250,000,000 as burn-in. The statistical difference between categories (migrants and non-migrants) was calculated as the proportion of the posterior in which the *r* scalar is estimated over 1 for the migrant partition. For the migrant partition to have significantly faster rates of mass evolution, the *r* scalar should be higher than 1 over 95% of the MCMC iterations (pMCMC < 0.05).

In the second approach, we evaluate Simpson’s filter-bridge hypothesis using the Phylogenetic generalized least squares (PGLS) between the path-wise rate of body mass evolution (transformed to $\log_{10}$) and the path-wise of n-continental-transitions. The path-wise rate of body mass is the sum of all the body mass evolution rate-scaled branches along the evolutionary path leading to individual species, i.e., the body mass changes accumulated between the root of the tree and each tip of the phylogeny (Baker et al. 2015). The path-wise of n-continental-transitions is the number of trans-continental dispersals accumulated between the root of the tree and each tip of the phylogeny. Therefore, there are 1,317 values of both variables. To get the path-wise of both variables, we use the function “nodepath” implemented in the package "ape" (Paradis & Schliep 2019), and the regression was evaluated with the function "pgls" implemented in the R-package “caper”

(Orme et al. 2013) using the tree with branches scaled by the rate of body mass evolution and restricting the parameter lambda = 1. We tested four additional models that include additive potential predictors of body mass evolution rate path-wise. These predictors are time and body mass due to the strong relationship between these variables framed in Cope's Rule. Models were tested with the function "pgls" implemented in the R-package “caper” (Orme et al. 2013) using the tree with branches scaled by the rate of body mass evolution and restricting the parameter lambda = 1. The best-fitted model was selected comparing the AIC parameter and the p-value of the predictor.

Hypothesis 2: The positive distance-evolution

To evaluate the relationship between the distance traveled and the body mass evolution rate across the 2,632 phylogeny branches, we run an OLS regression analysis in R-software, using the logarithm base 10 for both variables. Then, we evaluated the relationship between the path-wise distance traveled and the path-wise rate of body mass. The path-wise distance traveled is the sum of all distance-scaled branches along the evolutionary path leading to individual species. For this, we first replaced the branch lengths of the time tree with the distances estimated with the Geomodel. Then, we used the function “distRoot” implemented in the R-package “adephylo” (Jombart & Dray 2010) to obtain the distance each species traveled from the location of the most recent common ancestor (root) of the complete phylogeny. The relationship was evaluated in a PGLS where the body mass evolution rate path-wise is the response variable and the path-wise distance is the explanatory variable. We tested four additional models that include additive predictors that could increase the explanation of the path-wise of body mass evolution rate. These predictors are time and body mass (see above). Models were tested with the function "pgls" implemented in the R-package “caper” (Orme et al. 2013) using the tree with branches scaled by the rate of body mass evolution and restricting the parameter lambda = 1. The best-fitted model was selected, comparing each predictor's AIC parameter and p-value.

RESULTS

Dispersal estimations: Distances and ¿Trans-continental o intra-continental?

From the Geomodel output, we obtained 2,632 distances estimated (in kilometers) corresponding to each phylogenetic branch of the mammalian carnivores’ tree, supporting a model with significant variation, reaching magnitudes between 1.62 to 15,077 kilometers estimated in the distance between an ancestral and its descendant nodes. The frequency distribution of the distances estimated is asymmetric and biased to the left, showing that the short-distance dispersals (SDD) are much more frequent than long-distance dispersals (LDD; Figure 1).

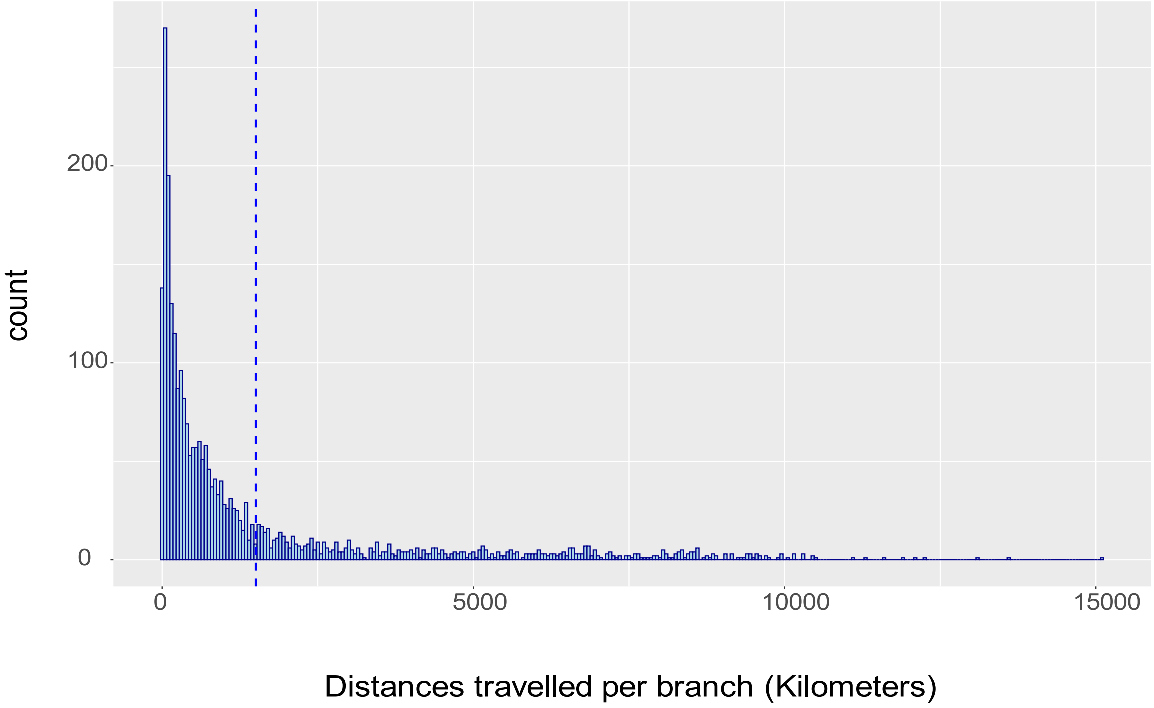

Figure 1. Frequency distribution of the Branch-wise geographic distances estimated with the Geomodel. The dashed blue line indicates the distribution mean.

350 of 2,632 (13.3%) distances estimated in the Geomodel correspond to trans-continental dispersal events ranging from 2,013 to 15,077 kilometers estimated. Meanwhile, most parts of the dispersal events estimated (86.7%) correspond to the movement of lineages inside the continental landmasses, ranging from 1.62 to 7,256 kilometers estimated. Therefore, most LDD corresponds to trans-continental dispersals (Figure 2a). Nevertheless, these categories are not phylogenetically clustered (Figure 2b). Of the 350 transcontinental events, 116 are between North America and Europe, 30 between North America and Asia, 87 between Europe and Asia, 54 between Europe and

Africa, 24 between Africa and Asia, 21 between North America and South America, and 18 are rare, i.e., between continent without geographical connections.

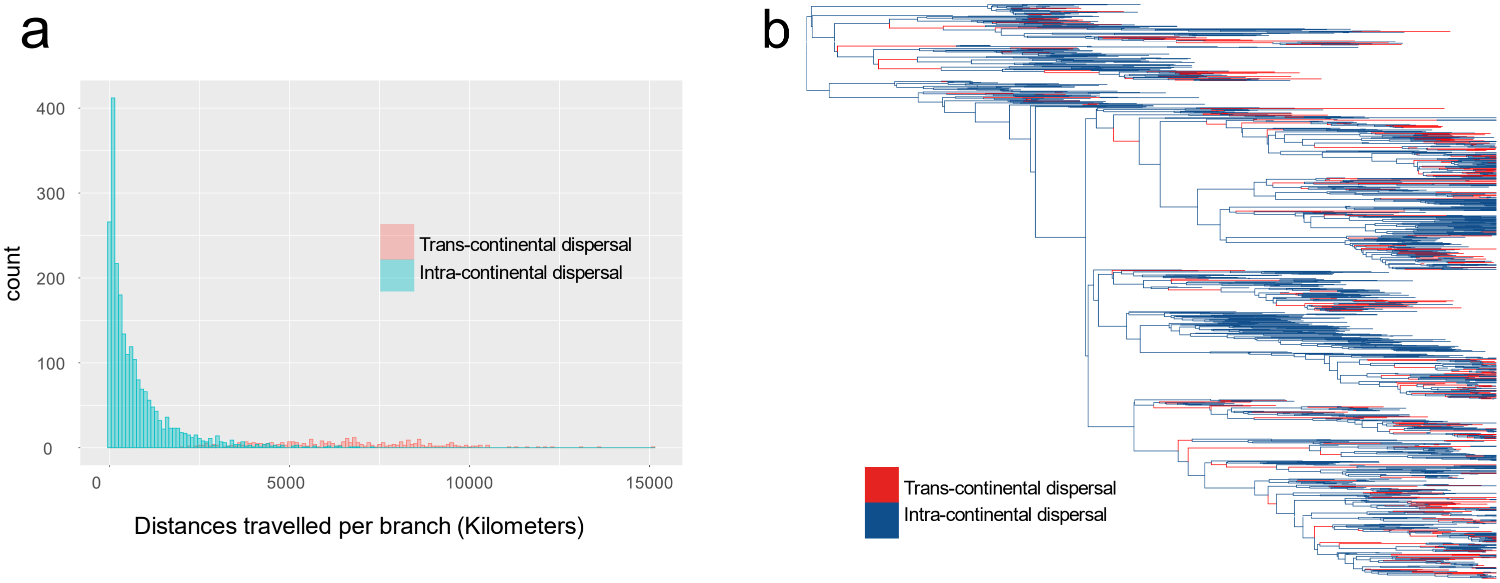

Figure 2. Branch-wise distances are categorized by "trans-continental" and "intra-continental" dispersals. a) Frequency distribution by categories; b) Phylogenetic tree with branches colored by categories.

Body mass evolution rate

Of the six body mass evolution models evaluated, the best-fitted is the VR applied in a phylogenetic regression model where body mass is predicted by time and a quadratic term for time [VR (Body mass ~ $\alpha + \beta_1(\text{Time})*\beta_2(\text{Time}^2)$)] (Table 1). From the output of the VR model, we obtained the amount of change accumulated by million years, i.e., the rate of body mass evolution, dividing the scaled branches by the branches of the time-calibrated tree. Of the 2,632 branches, 1,632 exhibited slower than expected body mass evolution according to BM, 367 branches had body mass evolution rates in line with BM, and 633 branches showed faster than expected body mass evolution according to BM

(Figure 3; Figure 4b). The branches where body mass evolved faster than expected by BM are clustered in the tree and correspond to follow groups: The Oxyaenidae† clade; Within the Hyaenodonta† clade: the Hyainailourinae† and Proviverrinae† subfamilies, and the genus *Hyaenodon*†; Within Carnivoramorpha, the Felidae family is the only one that shows faster body mass evolution in the Feliformia suborder, while Caniformia suborder shows faster body mass evolution in Canidae (genera *Vulpes* and *Canis*) and Mustelidae families. Within the Mustelidae family, the subfamilies Oligobuninae, Guloninae, and Lutrinae + Mustelinae (Figure 5c).

Table 1. Model comparison for the evolution of body mass. The log Marginal Likelihood (Marginal Lh), estimated by stepping-stone sampling, provides the model's support given the data and priors while accounting for the model parameter number. A higher value between two models, with a difference of 2 log units, support a given model. BM = Brownian Motion, VR = Variable Rate, bme= body mass evolution, α= the intercept of the regression, β_1, and β_2 = are the coefficients of the regression relating Time and Time^2 to the response variable.

Phylogenetic Model	**log Marginal Lh**	**α**	**β_1**	**β_2**	**R^2**
VR-model	-532.225	-0.111	-	-	-
BM-model	-729.685	-0.157	-	-	-
bme ~ $\alpha + \beta_1$(Time)					
VR-model	-493.531	-0.554	0.021	-	0.059
BM-model	-693.149	-0.728	0.021	-	0.041
bme ~ $\alpha + \beta_1$(Time) + β_2(Time^2)					
VR-model	**-492.922**	**-1.704**	**0.072**	**-0.0004**	**0.079**
BM-model	-689.351	-2.065	0.093	-0.0005	0.061

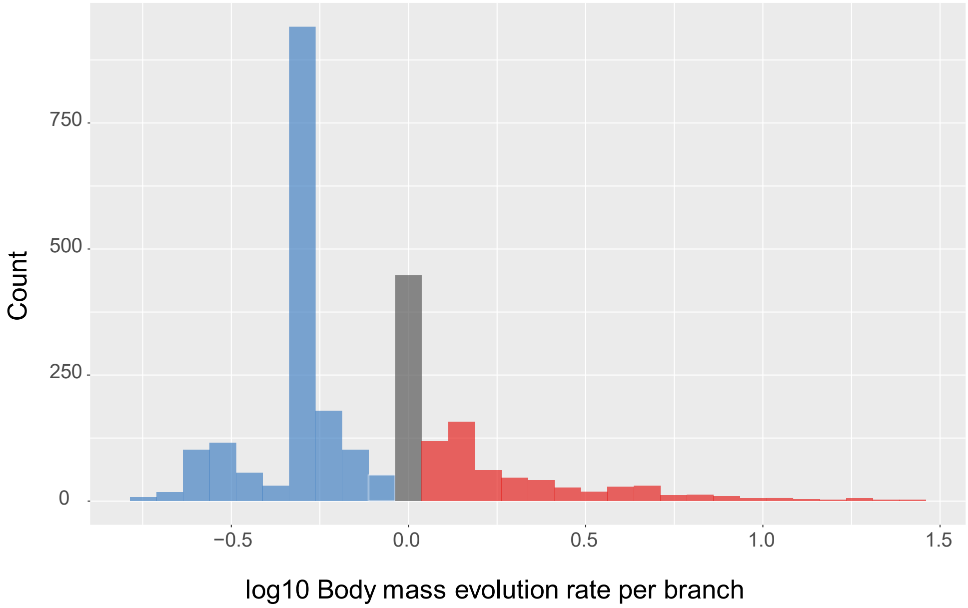

Figure 3. Branch-wise body mass evolution rate frequency distribution. Values are the log10 of the "r" scalar in the VR model. In blue, values < 0 (i.e., r<1) are branches where body mass evolved slower than expected by the BM model; In grey, values = 0 (i.e., r=1) are branches where body mass evolved under the BM model; In red, values > 0 (i.e., r>1) are branches where body mass evolved faster than expected by BM model.

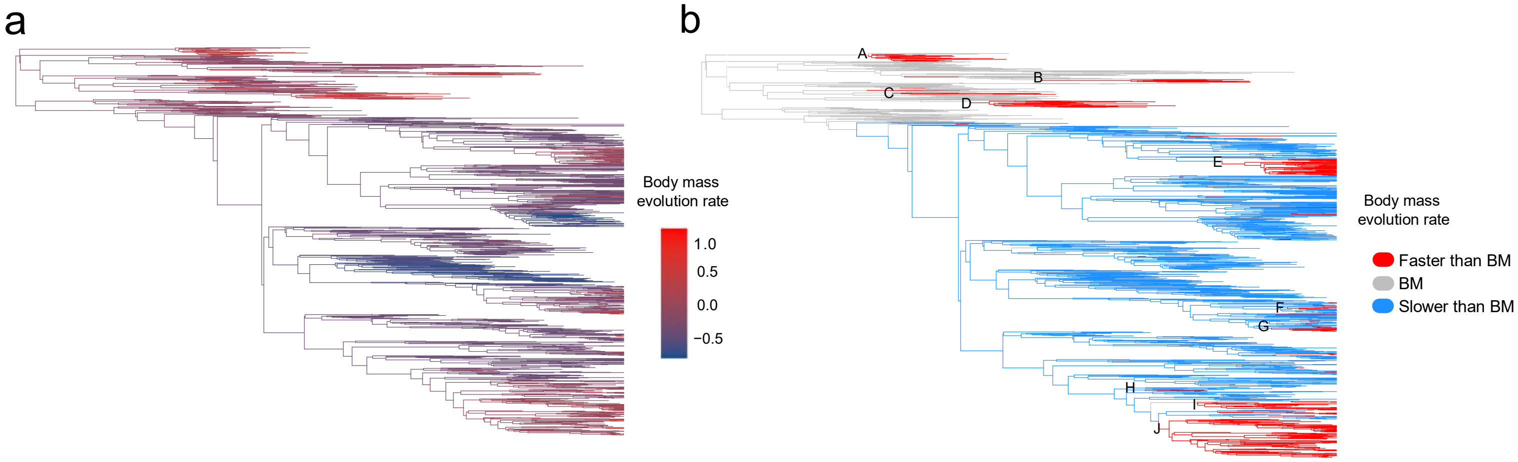

Figure 4. Body mass evolution rate across the mammalian carnivores time tree. a) Phylogenetic tree with branches colored given the rate of body mass evolution as a continuous variable; b) values of body mass

evolution rate colored by the categories, grey: constant rate, blue: rates lower than expected by BM, red: higher than expected by BM. A= Oxyaenidae, B= subfamily Hyainailourinae (Hyaenodonta), C= subfamily Proviverrinae (Hyaenodonta), D= genus *Hyaenodon* (Hyaenodonta), E= family Felidae (Feliformia), F= genus *Vulpes* (Canidae, Caniformia), G= genus *Canis* (Canidae, Caniformia), H= subfamily Oligobuninae (Mustelidae, Caniformia), I= subfamily Guloninae (Mustelidae, Caniformia), J= subfamilies Lutrinae + Mustelinae (Mustelidae, Caniformia).

Hypothesis 1: Simpson's filter-bridge.

From the VR model output, we obtained the amount of change accumulated by million years, i.e., the rate of body mass evolution; and from the Geomodel output, we obtained the categorization of dispersals as trans-continental ("migrant lineages") or intra-continental ("non-migrant lineages"), both variables for the 2,632 branches of the mammalian carnivores. Of the three Variable rates with branch-partition models evaluated, the best-fitted model includes the Time and the quadratic form of the Time (Table 2). Considering a threshold value of 0.05 (pMCMC < 0.05), our results show that 740 of the 1000 MCMC iterations (74%) have a stretched-branch > 1, and 260 (26%) have a compressed-branch < 1. Therefore, there is no evidence to support a faster or slower evolution process in the set of "migrant" branches compared to background rate ("non-migrant") branches. In other words, there is not significant difference in the body mass evolution rate among the two groups of lineages.

Table 2. Model comparison for the evolution of body mass using branch-partition. The log Marginal Likelihood (Marginal Lh) estimated by stepping-stone sampling, provides the model's support given the

data and priors. More positive values support a given model. Bmer = body mass evolution rate, α= the intercept of the regression, β_1, and β_2 = are the coefficients of the regression when including Time and Time^2 as predictors.

Phylogenetic Model	**log Marginal Lh**	**α**	**β_1**	**β_2**	**R^2**
bmer ~ α	-533.885	-0.113	-	-	-
bmer ~ α + β_1(Time)	-495.087	-0.599	0.017		0.061
bmer ~ α + β_1(Time) + β_2(Time^2)	-499.688	-1.704	0.072	-0.0004	0.082

According to our second approach to evaluate the filter-bridge hypothesis, our results show that the maximum path-wise trans-continental dispersals across the mammalian carnivores' tree is five and is the less frequent. Only twenty lineages show five trans-continental dispersals accumulated between the root and the tips of the tree. Therefore lineages that experienced few or no trans-continental dispersals accumulated are the most frequent (Figure 5).

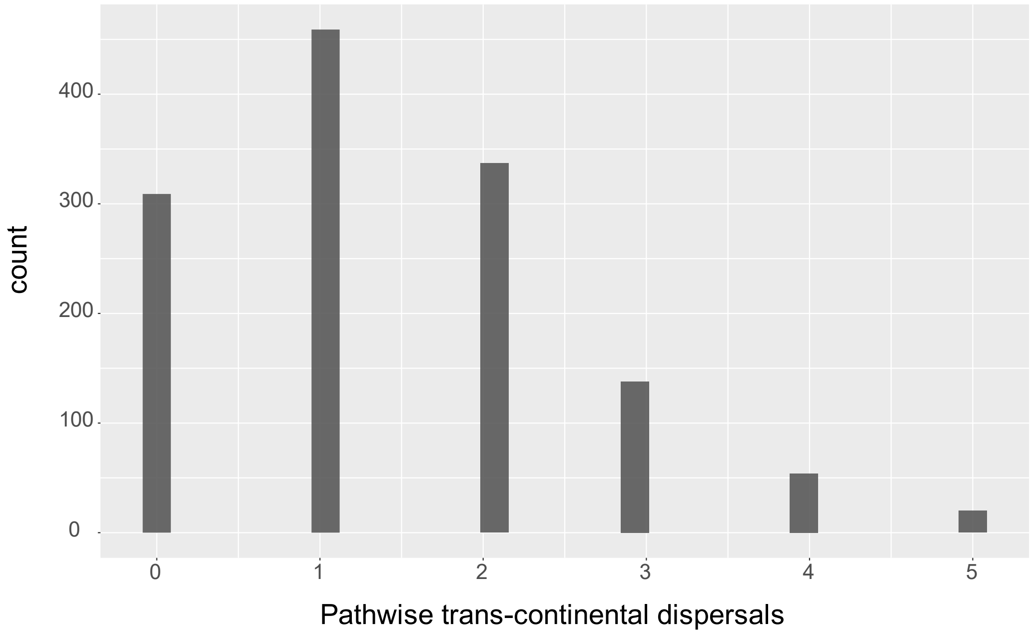

Figure 5. Histogram of the path-wise trans-continental dispersals estimated. Is the number of trans-continental dispersals accumulated between the root of the tree and each tip of the phylogeny.

The results of OLS analysis show a slightly positive (slope= 0.01) and significant (p-value= 0.00005) relationship between the path-wise body mass evolution rate and the path-wise of trans-continental dispersals (Figure 6). However, when considering the phylogenetic dependence of the species in the PGLS regression, the results show a negative (slope= -0.0007) and non-significant (p-value= 0.28) relationship between the path-wise body mass evolution rate and the path-wise trans-continental. Therefore, this second approach does not support the “Simpson” hypothesis either.

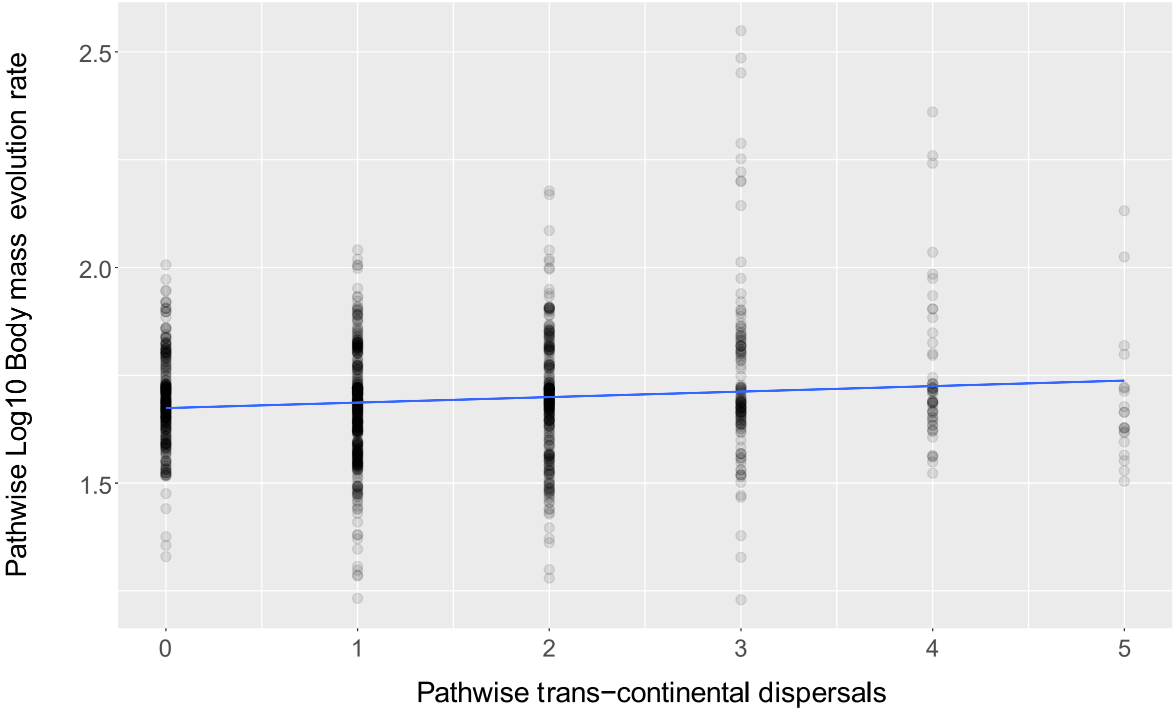

Figure 6. OLS between the path-wise body mass evolution rate and the path-wise trans-continental dispersals. The blue line is the predicted relationship given the inferred regression coefficients.

Hypothesis 2: The positive distance-evolution.

The OLS regression shows a positive (slope=0.06) and significant (p-value=1.15×10^{-13}) relationship between the distance traveled and the body size evolution rate across phylogenetic branches, considering the 2,632 branches of the phylogenetic tree (Figure 7). The estimated slope indicates that each unitary change of the $\log_{10}$ distances traveled is associated with an increase of 0.06 in the average $\log_{10}$ body size evolution rate. The intercept value of -0.278 indicate the average $\log_{10}$ body mass evolution rate when the distance estimated is 0, i.e., when there is no geographic movement between an ancestral and descendant node. The coefficient of determination R^2= 0.023 indicates that the model explains 2.3% of the total variability of the dependent variable.

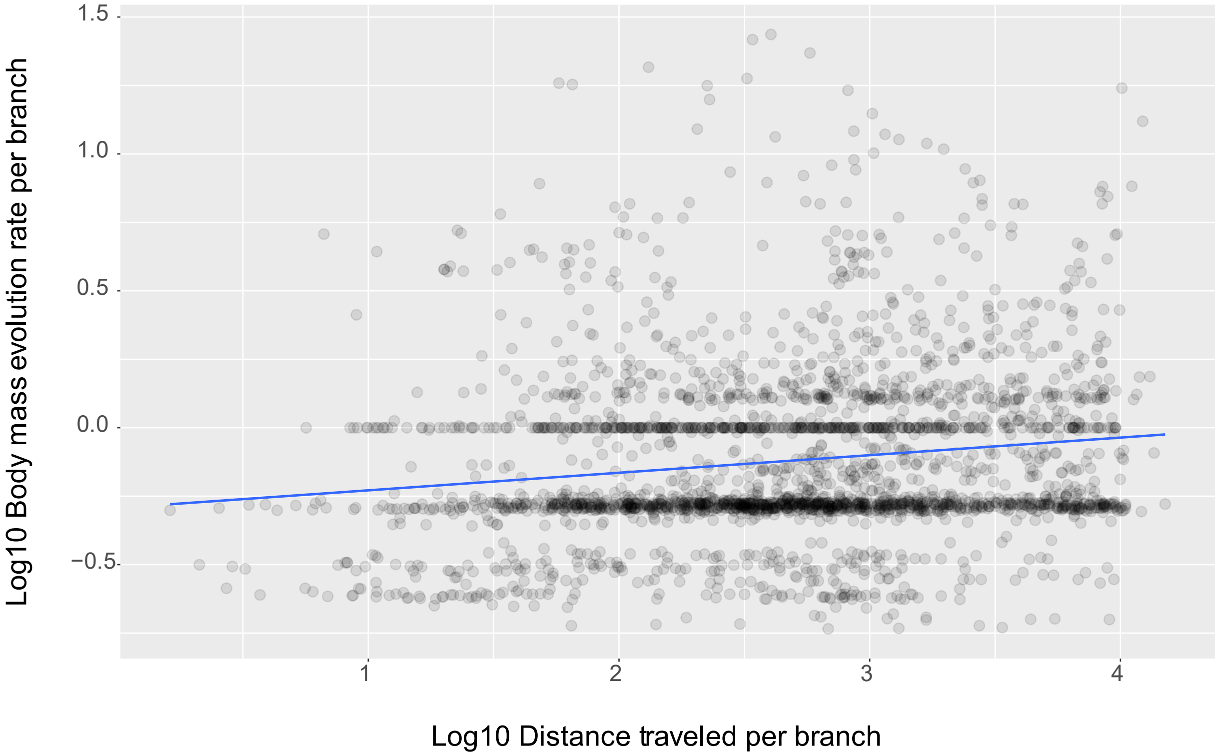

Figure 7. OLS between the distance traveled and the body size evolution rate (both transformed to $\log_{10}$). Each dot is one of the 2,632 phylogenetic branches. The blue line is the predicted relationship given the inferred regression coefficients.

Also, the OLS regression between the path-wise distance traveled and the path-wise rate of body mass evolution shows a positive (slope=0.21) and significant (p-value=$2x10^{-16}$) relationship, considering the 1,317 root-to-tips paths estimated (Figure 8). The estimated slope indicates that each unitary change of the $\log_{10}$ path-wise distances traveled is associated with an increase of 0.21 in the average $\log_{10}$ path-wise body size evolution rate. The intercept value of 0.8 indicates the average of the $\log_{10}$ path-wise the body mass evolution rate when the path-wise distance estimated is 0, i.e., when there is no geographic movement between the root and the tips. The coefficient of determination $R^2 = 0.38$ indicates that the model explains 38% of the total variability of the dependent variable.

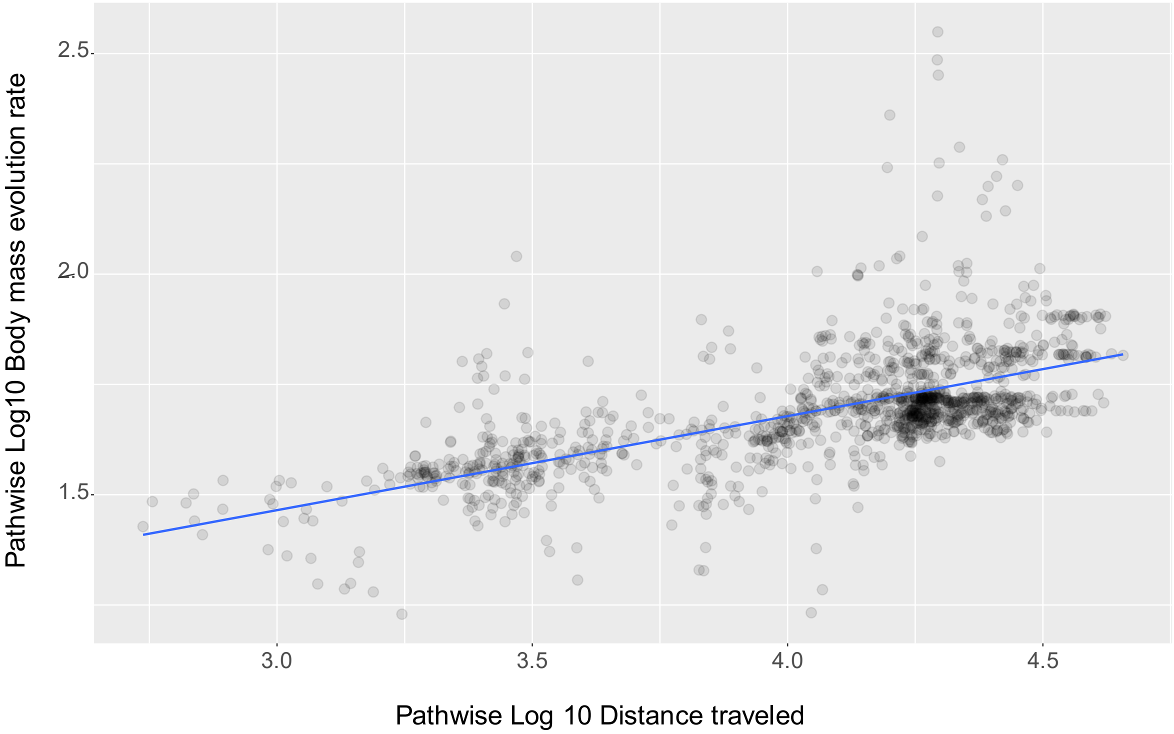

Figure 8. OLS between the path-wise distance traveled and the path-wise body size evolution rate (both transformed to $\log_{10}$). Each dot is one of the 1,317 root-to-tip paths estimated. The blue line is the predicted relationship given the inferred regression coefficients.

Then, when we evaluated the relationship in a phylogenetic context, the PGLS regression between the path-wise distance traveled and the path-wise rate of body mass evolution showed a slightly positive (slope=0.05) and significant relationship (p-value=2×10^{-16}). The coefficient of determination $R^2= 0.07$ indicates that the model explains 7% of the total variability of the dependent variable. The mass and time of the species included as additive variables to the model are significant predictors increasing the coefficient of determination and the model fit (Table 3). Body mass has a positive relation (slope= 0.02) and Time a negative (slope= -0.005) with the path-wise body mass evolution rate (Figure 9).

Table 3. PGLS models to predict the pathbmer (path-wise body mass evolution rate) given the following predictors: pathdist= path-wise distance traveled; n° trans= path-wise of the trans-continental dispersal; time= age of the species and mass= body mass of the species. The number of asterisks is the different degrees of statistical significance: ***=99.99%, **= 99.9%, and * = 99%.

Parameters	Model 1 pathbmer ~ pathdist	Model 2 pathbmer ~ pathdist + n° trans	Model 3 pathbmer ~ pathdist + n° trans + time	Model4 pathbmer ~ pathdist + n° trans + mass	Model5 pathbmer ~ pathdist + n° trans + time + mass
Intercept	1.24***	1.24***	1.7***	1.25***	1.7***
Slope pathdist	0.05***	0.05***	0.009**	0.048¨***	0.009**
Slope n°trans	-	-0.0009	-0.0004	-0.001	-0.0004
Slope time	-	-	-0.005***	-	-0.005***
Slope mass	-	-	-	0.02***	0.004*
Model summary	Model 1	Model 2	Model 3	Model 4	Model5
F-statistic	99.26	50.58	833.4	61.04	628.9
DF residual	1315	1314	1313	1313	1312
Adjusted R^2	0.07	0.07	0.65	0.12	0.66
AIC	-5414.873	-5414.707	-6719.207	-5486.980	-6723.072
Δ AIC	1308.199	1308.365	3.86	1236.092	0

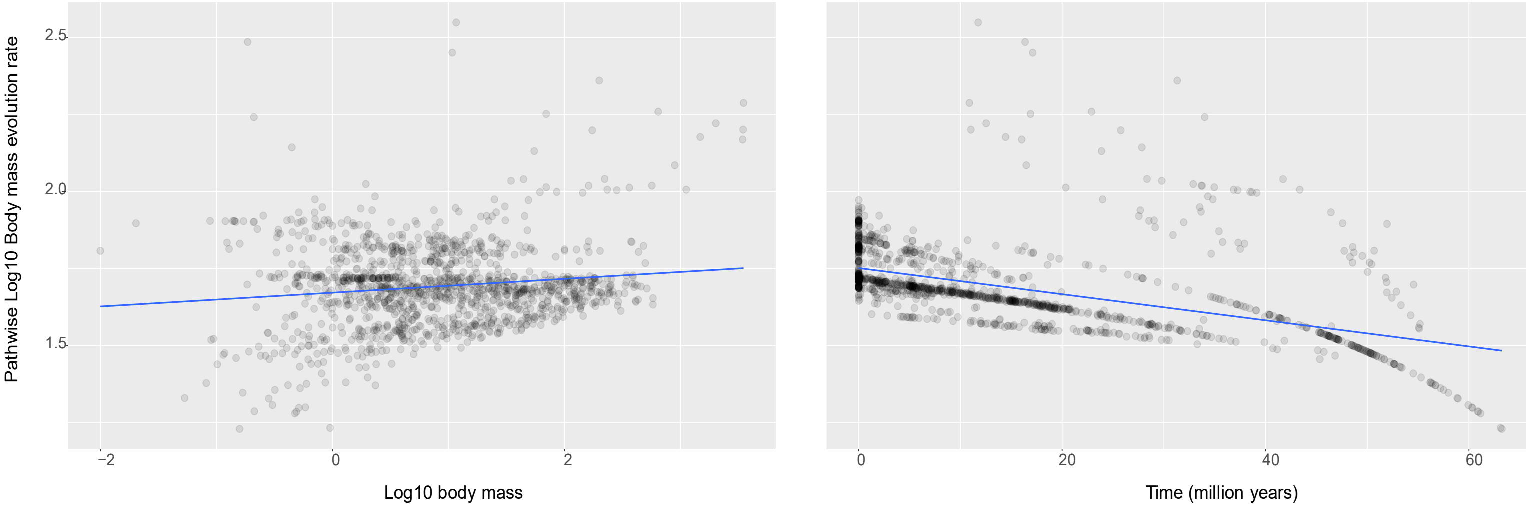

Figure 9. OLS between the path-wise body mass evolution rate as the response variable and two significant predictors. Left: Regression between the path-wise body mass evolution rate and the body mass of the species (both transformed to log10); Right: Regression between the path-wise body mass evolution rate and the Time of the species. The blue line is the regression line that best fits the observed data in terms of minimizing squared errors.

DISCUSSION

Our results show a significant positive relation between the path-wise of dispersal ability and the path-wise of body mass evolution rate, supporting the "positive dispersal-evolution" hypothesis proposed. Thus, the LDDs as a biogeographical process explain the body mass fast evolution and diversity in mammalian carnivores. Although most parts of the LDD estimated are trans-continental dispersals, crossing between different continents *per se* does not increase the rate of body mass evolution in carnivores. Therefore, the rate of body mass evolution will increase depending only on how far away the new environments colonized are. In other words, the fast evolutionary change in mammalian carnivores is partly a result of the biological filters that imply the long geographical movement even inside of each continent. Also, the effect of LDDs is involved mainly in the evolution of some descendant clades of migrant lineages, i.e., LDDs could be only a contingent event that facilitates the evolution of clades after their arrival to a new far geographical area. In these cases, the journey is only part of the ecological opportunity before an adaptive process.

The long-distance dispersals (LDD)

This is the first study that estimates the historical species dispersal distances in mammalian carnivores' extant and extinct diversity and their implications on the group's evolutionary history. There are several reasons why this relationship was previously despite the carnivores' relevance for macroecology and macroevolution (Meiri et al. 2004; Van Valkenburgh et al. 2004; Pires et al. 2015, 2017; Silvestro et al. 2015; Slater & Friscia 2018, 2019; Faurby et al. 2019). First, there are inconsistencies in measurements and definitions of dispersal. Second, there are difficulties in collecting empirical data owing to the ‘once in a lifetime nature of dispersal events in many species and, third, the inability of most studies to capture long-distance dispersal (LDD) events (Koenig et al 1996; Ferriere et al. 2000; Bowman et al. 2002; Whitmee & Orme 2013; Stevens et al. 2014). Identifying long-distance dispersals (LDDs) is crucial for understanding macro-scale biodiversity evolution, despite their rarity compared to short-distance dispersals (SDDs). In fact, as our results support, LDDs are one of the species-level properties that provide several lineages the opportunities for rapid access to climatically suitable habitats, for instance, to colonize a new continent when the geological and climatic conditions create a land bridge (Böhning-Gaese et al. 2006; Whitmee & Orme 2013). In this sense, our results also show that most parts of the LDD estimated are trans-continental dispersals but are not exclusive, given that some LDD dispersals occurred inside the continental landmasses: for example, the journey within Africa and North America, from north to south. An alternative formulation would be that the true barrier in some cases was not the presence of a stretch of the sea but some less obvious environmental factor, such as climate or vegetation, with shows a clear gradient of latitudinal changes across the globe (Fischer 1960; Brodie & Mannion 2023). Also, the fact that LDD dispersals estimated have a random distribution across the phylogeny suggests that experiencing an LDD dispersal is not a process with a phylogenetical tendency (i.e., of a positive association between the probability of continental transitions with the degree of species relatedness), but rather a spontaneous response to the possibility to move across a geographically near path (corridors or "bridges"). On the other hand, the geographic distance to the corridors or "bridges" may be far away making it inaccessible for some species and they cannot use a bridge that they cannot reach (Simpson 1940). Then, let us suppose that the median value of the ancestral location estimated for each lineage is the "monument spot" mentioned by Simpson (1940), alluding to the “center or cradle of origin” of a species (in our case, a meta-populational lineage as the definition of species concept). Thence, species tend to spread steadily in all directions until it encounters insuperable geomorphological or climatic barriers. Additionally, species have inherently different capacities to move far beyond these barriers when the conditions are adequate, i.e., populations within species must move from place to place, and some must travel where their immediate ancestors had never been. With each new step of their geographical journey, the new populations face new environmental conditions that imply the consequent adaptation reflected here in the fast body mass evolution towards some direction.

The LDDs are associated with phenotypic selection.

Several recent works link the intensity of natural selection that leads to adaptations with the rates of morphological evolution (Eastman et al. 2011; Venditti et al. 2011; Revell et al. 2012; Thomas & Freckleton 2012; Kutsukake & Innan 2013, 2014; Kratsch & McHardy 2014; Rabosky 2014; Baker et al. 2015), identifying exceptional shifts in rate as indicative of positive phenotypic selection at a macroevolutionary scale (Baker et al. 2015). Here, we identify faster path-wise body mass evolution rate in several independent lineages of mammalian carnivores and the biogeographical process that helps to explain this differential rhythm of changes and, therefore, the diversity of body mass. Repeated LDD events throughout history caused fast evolution in recent species, giving this relationship a historical component. At macroevolutionary scales, species (meta-populational lineages) moving geographically from their center of origin experience population turnover (through the birth and death of the cohorts) as long as they move to far new geographical areas. This implies that the new population cohorts rapidly adapt their physiology and ecology to these new environments, contrary to "philopatric species" that change with the rhythm of the local environment. Moreover, the effect of this fast evolution (adaptions) associated with the LLD experienced is maintained even when the body mass and age of the species are considered for explaining the path-wise body mass evolution rate.

Larger and recent species have faster body mass evolution, which agrees with Cope's rule (Cope 1896; Kingsolver & Pfennig 2007; Hunt et al. 2010). Baker et al. (2015) showed that Cope's rule is most likely to be explained by repeated adaptive responses to new selective circumstances, such as competition (Benson et al. 2014) or climate changes (Hunt & Roy 2006; Hunt et al. 2010). Raia et al. (2012) suggested that Cope’s rule is explained by increasing clade-level niche expansion during the Cenozoic because of the ecological specialization of species. Therefore, our results allow us to add that the repeated new ecological opportunities, and circumstances that lineages found each time they traveled long distances to colonize new geographical areas across their evolutionary history, help explain this fast evolution pattern in body mass. Finally, the fact that body mass evolution has a clustered distribution across the phylogeny is indicative that the effect of the selective pressures due to these biogeographical events seems not always to be expressed in the same "migrant" lineage or phylogenetic branch as expected by a filter-bridge effect. The effect seems to be in some descendant clades, i.e., LDDs could be only a contingent event that facilitates the evolution of clades after their arrival to a new far geographical area. In these cases, the journey is part of the ecological opportunity before an adaptive process (Schaeffer 1948; Van Valen 1971; Sanderson & Donoghue 1994; Hunter & Jernvall 1995; Mahler et al. 2010; Slater 2015).

In the mammalian carnivores

The oxyaenids and proviverrines seem to be the exception in that almost the complete clades show a fast evolution in body mass. Nevertheless, they do not experience longer dispersal distances. Oxyaenidae was a clade with relatively constrained geographic distances dispersals, mainly within North America, averaging 483 kilometers traveled between the ancestral and descendant nodes in the continent. Even so, some lineages (the genus *Palaeonictis*) crossed to Eurasia during the Paleocene-Eocene thermal maximum (PETM), and previous works had already suggested these migrant lineages decreased in body size during this period (Heinrich et al. 2008; Chester et al. 2010) showing a "filter-bridge" effect during the dispersal. Proviverrinae is a subfamily considered to be endemic to Europe, where it underwent radiation (Solé 2013) and a notable increase in body masses in a short time: Some species weighed about 10 kg, whereas the earliest proviverrines weighed less than 1 kg (Solé et al. 2014). The North American oxyaenids and the European proviverrines are older groups (59 and 56 mya, respectively) that experienced mainly short dispersal distances; therefore, their radiation and accelerated body mass evolution are not related to LDD events confirming that this relation is expressed mainly in recent lineages. Now, about the clades with the effect of LDDs. Hyainailourinae is a subfamily of hyaenodonts with some of the largest terrestrial carnivorous mammals ever known (Savage 1973; Lewis & Morlo 2010; Solé et al. 2015), and that dispersed across Europe, Asia, North America, and Afro-Arabia (Borths & Stevens 2019). Particularly, the hyainailourine subclade that shows faster body mass evolution arrived in Afro-Africa from

Europe 26 mya (Late Oligocene), and then experienced several dispersals between Afro-Africa and Eurasia in both directions during the Miocene (results of the first chapter), that was an interval of increasing tectonic and faunal connectivity between these two landmasses (Sen 2013), and at the same time during the Miocene, the largest hyainailourines appeared within this subclade (Savage 1973; Ginsburg 1980; Morales & Pickford 2017). *Hyaenodon* is a large genus of the subfamily Hyaenodontinae that originated 46 mya in North America from a direct European ancestor. *Hyaenodon* reached a widely distributed across the whole northern hemisphere from the Late Eocene to Early Miocene (Solé et al. 2018), with at least nine dispersal events between North America and Eurasia (results of the first chapter). Their body size ranged from marten-sized (*H. microdon*) to bear-sized forms (*H. gigas*). The few dwarf species: *H. filholi* from Europe; *H. eminus* and *H. chunkhtensis* from Asia, and *H. raineyi* from North America (Lavrov 2019), come directly from a trans-continental dispersal between Eurasia and North America except for *H. rainey,* whose direct ancestor traveled around 3000 kilometers from northern North America to southern North America (results of the first chapter). Within Carnivoramorpha, Felidae is a family that experienced several trans-continental and long-dispersal events since their origin in Europe 29 million years ago, even recently, being the unique feliform family that colonized South America more once time. This accumulative exploration of new geographical areas across time and the independent arrival towards the same continent within the family (for example, 14 times to Africa) acted as repeated ecological opportunities before an adaptive process expressed in the fast body mass evolution in the wide subclade that led to extant diversity, not so in the extinct subfamily

Machairodontinae. In felids, the relation seems not to be only accumulative (the path-wise rate of evolution) but also a direct and recent relation in some lineages between migration and increase their body mass. Previous works have already found exceptional, recent, and directional increases in the rate of body mass evolution in the branches reaching the big cats of the genera *Panthera*, *Acynonyx,* and *Puma* (Venditti et al. 2011; Harano & Kutsukake 2023), and effectively the most part the species within these genera dispersed recently (since less than 4 mya) long distances, for example, *Panthera leo*, *Panthera pardus*, and *Acynonyx jubatus* colonized Africa independently from Europe averaging 4300 kilometers traveled (results of the first chapter). Currently, the felids vary extensively in size, ranging from the black-footed cat (*Felis nigripes*) and rusty-spotted cat (*Prionailurus rubiginosus*), weighing less than 2 kg, to the some *Panthera* species, which can weigh more than 300 kg (Turner & Antón 1998; Macdonald et al. 2010; Venditti et al. 2011; Cuff et al. 2015; Sunquist & Sunquist 2017). Within Caniformia, the Caninae subfamily of the canid's family shows independent faster body mass evolution in several branches, mainly within the genus *Canis*. Currently, the major amplitude of body sizes in the family Canidae is in Caninae, ranging from approximately 1 kg (*Vulpes zerda*) to 35 kg (*Canis lupus*; Wang 2008). Although previous works have not evaluated the effect of the LDD on the morphological evolution of this group, a recent work proposed that the Bering Strait and the Isthmus of Panama formation and the geographic characteristics of the continents at the time of the canines' invasion suggest an ecological opportunity at least for the evolutionary radiation (Porto et al. 2023). Our results show that since their origin 33 mya (considering the genus *Leptocyon*), Caninae experienced several LDD and trans-continental events, and lineages implicated in the dispersals between Eurasia and another continent (North America and Africa) are related to this fast evolution. Of the lineages implicated in the Great American Biotic Interchange (GABI), only the genus *Dusicyon* evolved quickly. Notably, two insular species as independent lineages show faster body mass evolution, the recently extinct Falkland Islands wolf (*D. australis*) and the Channel Islands fox (*Urocyon littoralis*). The first and their continental sister species *D. avus* are bigger than their closest relatives, meanwhile that *U. littoralis* is a morphologically smaller species, approximately two-thirds the size of its progenitor, the mainland gray fox, *U. cinereoargenteus* (Collins 1982, 1991; Wayne 1991). Also, within Caniformia, the endemic South American genus *Arctotherium* shows fast body mass evolution related to their arrival to South America after traveling 8030 kilometers from North America (results of the first chapter). This LDD event seems to act as an ecological opportunity of arriving to a new far geographical area to experience an adaptive process here expressed in the fast body mass evolution. These South American species quickly ranged in size from the relatively small *A. wingei* (around 150 kg) to the giant short-faced bear *A. angustidens*, which may have attained body masses exceeding 1000 kg (Mitchell et al. 2016). Finally, within Caniformia, the Mustelidae family shows fast body mass evolution in the almost complete clade. Since their origin in North America 28 mya, mustelids have experienced more than seventy trans-continental dispersals and thus repeated LDD events across history that led to the most recent species expressing a fast evolution. Several repeated dispersals have been reported from Eurasia to Africa (Werdelin 2003) and to North America via the Bering land bridge (Baskin 1998). Also, several dispersals to South America (Marshall & Sempere 1993; Coates & Obando 1996). Most parts of these LDD occurred during the Middle Miocene, and recently, Law (2019) found that within extant mustelid subclades (particularly Ictonychinae, Mustelinae, and Lutrinae) the evolutionary shifts towards small body sizes occurred during the Mid-Miocene Climate Transition (15.97–11.61 mya). Among the extinct genera known from Late Miocene deposits in Africa that may have arisen from Eurasian immigrants are the gigantic *Ekorus*, the largest mustelid discovered thus far (Koepfli et al. 2008).

Although this research did not assess the direction of the evolution, we show that sporadic biogeographical LDD events are involved in the fast evolution of the highly discrepant body sizes of the mammalian carnivores that are a manifestation of adapting to their respective niche, i.e., each size has its intrinsic ecological advantages. Small carnivores have better reproductive efficiency, access to a wider variety of food, and a greater ability to respond to environmental emergencies than larger carnivores (Moors 1980; Blanckenhorn 2000). In contrast, large body size can also bring many benefits, including the ability to exploit vast food resources, increased competitiveness, increased defense against predation, and extended longevity (Hone & Benton 2005; Vermeij 2016; Huang et al. 2021).

CONCLUSIONS

Our results show that long-distance dispersals (LDD) as a biogeographical process at the macro-scale explain the fast body mass evolutionary change found in several independent and mainly recent lineages of mammalian carnivores and thus their highly discrepant body sizes. These results do not disagree with the "Simpson's filter bridge" theoretical concept because we found some transcontinental branches with fast body mass evolution. However, the fact is that the crossing between different continents *per se* is not the cause of the increase in the rate of body mass evolution in carnivores. Also, we show that the effect of the selective pressures due to these biogeographical events seems not always expressed in the same "migrant" lineage or phylogenetic branch. However, instead, the effect seems to be in some descendant clades, i.e., LDDs could be only a contingent event that facilitates the evolution of clades after their arrival to a new far geographical area. In these cases, the journey is part of the ecological opportunity before an adaptive process.

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GENERAL CONCLUSIONS

The main historic scientific achievement has gone hand in hand with the innovation of methodological approaches. In comparative evolutionary biology, these innovations generally take into account the complex nature of biogeographical evolutionary processes as model assumptions. This allowed the testing of classic naturalist hypotheses that could not be evaluated in the past. Based on the integration of the geographical and evolutionary information of both extinct and extant diversity, in a framework that considers aspects of nature that had not previously been included in the modeling, this thesis postulate that allows establishing the center of origin, in several cases in a new geographical point, of the early and recent lineages of terrestrial mammalian carnivores at global scales, estimating the geographical distance traveled of the descendant lineages across the curved Earth and considering the tectonic movement. This estimation, for the first time, of the geographical distances traveled for all lineages and the identification of the trans-continental dispersals, may be an essential approach for macro-scale studies in any taxonomic group that searches know the historical movement of biodiversity across the globe.