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Influencia de los cambios climáticos globales en la estructura de las comunidades de mamíferos del Neógeno-Cuaternario

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PRESENTADA POR

Blanca A. García Yelo

Directores

Jorge Morales Romero
Manuel Hernández Fernández

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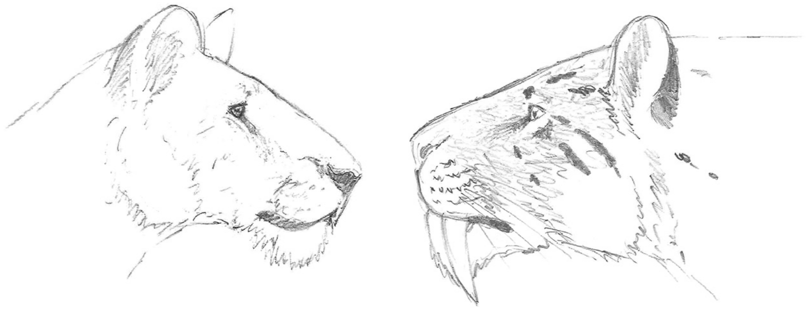

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Blanca A. García Yelo

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Jorge Morales Romero
Manuel Hernández Fernández
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Jorge Morales Romero	Manuel Hernández Fernández	Blanca A. García Yelo

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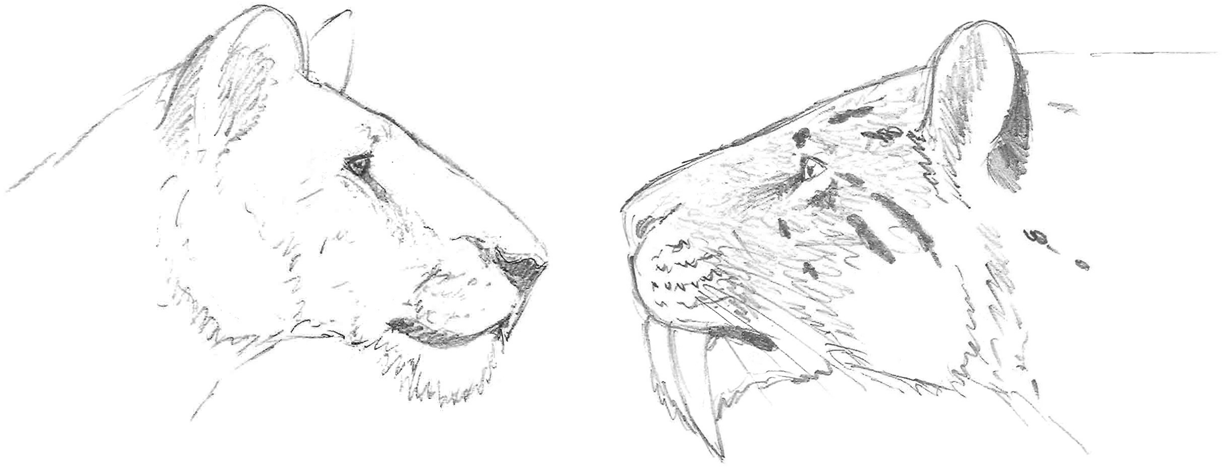

Blanca A. García Yelo

Directores de Tesis
Jorge Morales Romero
Manuel Hernández Fernández

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A mi familia y amigos.

ÍNDICE.

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RESUMEN / ABSTRACT.

RESUMEN

Título: Influencia de los cambios climáticos globales en la estructura de las comunidades de mamíferos del Neógeno-Cuaternario

Introducción

El objetivo principal de esta tesis es determinar cómo los cambios en el clima influyen en la estructura de las comunidades de mamíferos, un grupo con una alta diversidad, tanto taxonómica, como ecomorfológica, sino también al peso que han tenido en el desarrollo social, cultural y económico del ser humano. Además, dentro del grupo de los mamíferos, incidimos especialmente en el estudio del conjunto de los carnívoros (orden Carnivora) que, debido a su escasa representación en el registro fósil, son frecuentemente excluidos de los trabajos de inferencia paleoambiental y paleoecológica. Siempre se ha considerado que su ecología, fuertemente condicionada por la disponibilidad y el comportamiento de sus presas, es independiente del medio en el que habitan. Sin embargo, los carnívoros presentan una morfología específica, que refleja un alto grado de adaptación a la caza, lo que nos hizo replantearnos esa supuesta independencia relativa al medio en que realizan esta actividad.

Para analizar cómo influye el clima en la estructura de las comunidades de mamíferos, empleamos metodologías de inferencia ambiental tanto clásicas, como de nuevo desarrollo.

Síntesis

En el capítulo 2 analizamos la capacidad los cenogramas, una metodología basada en el estudio de la distribución de tamaños corporales de las especies, para describir las relaciones que se establecen entre los predadores y sus presas en las comunidades de mamíferos terrestres. Partiendo de la idea original planteada por Valverde, tratamos de contrastar dos hipótesis: a) en la distribución de tamaños corporales de las presas se produce un salto en torno a las tallas medias, asociado a la presión que ejercen los predadores sobre las especies de tamaño medio y, b) asociado a este desplazamiento, se produce el desarrollo secundario de un salto en la distribución de tamaños corporales de los predadores, como resultado de la carrera de armamentos que se establece entre ambos gremios.

Para llevar a cabo esta investigación estudiamos la estructura de los cenogramas de 100 localidades uniformemente distribuidas en la superficie terrestre, excluyendo Australia. Una vez construidos los cenogramas, calculamos la magnitud del salto, tanto en presas como en predadores, así como el tamaño medio de los distintos grupos tróficos. Mediante análisis de regresión lineal simple relacionamos, en primer lugar, la magnitud del salto en presas con el peso medio de los predadores y, en segundo lugar, la magnitud del salto en predadores con la del salto en presas. Posteriormente, con el objetivo de determinar la influencia del clima sobre estas interacciones, realizamos una serie de análisis de regresión múltiple por pasos en los que, a parte de relacionar las variables anteriormente citadas, incluimos una serie de factores climáticos que resumen las características ambientales básicas del medio. Finalmente, considerando los posibles efectos diferenciados de las glaciaciones del Pleistoceno, repetimos los análisis a dos escalas geográficas diferentes, global y latitudinalmente.

Los resultados obtenidos en el capítulo 2 mostraron una relación significativa, aunque débil, entre la continuidad en distribución de tamaños corporales de las presas y el tamaño medio de sus predadores a escala global y latitudinalmente. Dicha relación está controlada por factores ambientales, principalmente la temperatura y la estacionalidad del medio. Sin embargo, no detectamos relación significativa alguna entre la distribución de tallas de los predadores y la de sus presas asociada al efecto de la "carrera de armamentos". La aparición de un salto en la distribución de tallas de los predadores está condicionada, por el contrario, por factores asociados a la temperatura del medio, y sólo para las regiones tropicales del planeta.

A tenor de estos resultados, podemos desechar las hipótesis iniciales propuestas por Valverde. No existe una relación de tipo evolutivo, asociada a carrera armamentística, entre las distribuciones de tamaños corporales de predadores y presas. La estructura de tamaños corporales de ambos gremios está, por el contrario, condicionada por factores ambientales, particularmente la temperatura y la estacionalidad.

En el capítulo 3, analizamos cómo la estructura de las comunidades de mamíferos del Aragoniense medio de la cuenca de Madrid (Península Ibérica), definida por sus cenogramas y sus espectros de tamaño corporal, cambió como resultado de los cambios ambientales acaecidos en el Mioceno medio. Comparamos la estructura de las comunidades de seis yacimientos presentes en la cuenca de Madrid: Estación Imperial, Paseo de las Acacias, la asociación de Arroyo del Olivar-Puente de Vallecas, Somosaguas, Paracuellos 5 y Paracuellos 3. Para ello, empleamos

la información climática y faunística de las 100 localidades actuales y, mediante análisis discriminantes, establecimos una relación estadística significativa entre el bioma en el que habita la comunidad y su estructura, teniendo en cuenta sus diferentes historias biogeográficas

Según nuestros resultados, observamos que las faunas de mamíferos del Aragoniense de la Comunidad de Madrid reflejan un predominio de ambientes semiáridos, con varios pulsos de mayor aridez a lo largo del registro. Partiendo de unas condiciones áridas y abiertas, se produjo un primer cambio hacia condiciones relativamente más húmedas y con un mayor grado de forestalidad. Seguidamente, detectamos un retorno hacia condiciones más abiertas y áridas, que coincide temporalmente con el evento de enfriamiento global del Mioceno medio. Finalmente, las condiciones se estabilizaron, reflejando nuevamente un ambiente relativamente más húmedo y cerrado.

Por otro lado, en el capítulo 4 desarrollamos una nueva metodología de inferencia ambiental, los grupos funcionales de carnívoros, que permite estudiar la estructura de aquellos yacimientos excepcionales de carnívoros donde la fauna de herbívoros es habitualmente escasa. Esta metodología permite agrupar las 250 especies de carnívoros terrestres en 11 grupos según su tamaño corporal, tipo de dieta y locomoción, describiendo así la estructura de la comunidad de diferentes faunas y permitiendo determinar la existencia de una relación estadística entre esta y el clima.

Nuestros resultados muestran como tanto el tipo de dieta, como la locomoción, son los factores ecológicos más determinantes en el proceso de asociación. Esta preponderancia sobre el peso está relacionada con las limitaciones que imponen ambos factores en el balance energético de las especies. Posteriormente, y sirviéndonos de los listados faunísticos de las 100 localidades mencionadas en el capítulo 2, definimos la estructura funcional de las faunas de carnívoros de estas comunidades como el espectro funcional de cada comunidad (porcentaje de especies presentes en cada grupo funcional). Seguidamente, mediante un análisis de tipo ANOVA realizado sobre los espectros funcionales de las 100 localidades actuales, comprobamos la señal bioclimática de cada grupo funcional, observando como ningún grupo caracterizaba específicamente a un determinado tipo de bioma. En consecuencia, realizamos un análisis discriminante para poder establecer una relación entre el tipo de bioma y el espectro funcional de carnívoros de cada localidad. Además, como en el caso del capítulo 3, repetimos los análisis separando las localidades por regiones biogeográficas, con el objetivo de considerar la historia geológica y climática específica de cada una de ellas. Nuestros resultados nos permitieron observar que los factores que regulan los patrones de estructuración de las comunidades son distintos según nos encontremos en regiones tropicales o templadas. Mientras que las glaciaciones del Pleistoceno, junto con la presencia de barreras físicas, condicionaron en gran medida la estructura de las comunidades de carnívoros del Holártico, en las regiones tropicales la estructura de las comunidades de carnívoros está principalmente condicionada por alta diversidad específica presente en estas regiones.

En el capítulo 5, una vez confirmada su utilidad para inferir ambientes (biomas), aplicamos los grupos funcionales de carnívoros sobre las faunas de carnívoros presentes en los diferentes pozos de brea del yacimiento californiano de Rancho la Brea. Esto nos permitió analizar cómo los cambios climáticos asociados a las glaciaciones del Pleistoceno, junto con el posterior calentamiento del Holoceno, afectaron a la comunidad de carnívoros del suroeste norteamericano en los últimos 30.000 años. Para ello, comparamos la estructura de las comunidades, descrita por su espectro funcional, presentes en varios pozos de Rancho la Brea (California, Estados Unidos), junto con la de la fauna de carnívoros que encontramos actualmente en Los Ángeles (California, Estados Unidos).

En primer lugar, mediante un análisis morfofuncional, determinamos las características ecológicas (dieta, locomoción y tamaño corporal) de las especies de carnívoros presentes en los distintos yacimientos. A continuación, realizando un análisis discriminante, asignamos cada especie a un grupo funcional determinado, definiendo así el espectro funcional de cada pozo. Por último, y sirviéndonos nuevamente del análisis discriminante, comparamos dichos espectros con los de las comunidades actuales del Neártico, pudiendo así inferir el clima (tipo de bioma) asociado a cada yacimiento.

Finalmente, el análisis delos cambios en la estructura de la comunidades de carnívoros presentes en los diferentes pozos de Rancho la Brea reflejaron como, en los últimos 30.000 años, dos grandes alteraciones ambientales modificaron el paisaje del suroeste de Norteamérica. Inicialmente, la mayor aridez impuesta por las glaciaciones pleistocenas provocó el desarrollo de un bosque de matorral mediterráneo. Un cambio hacia condiciones de mayor humedad, asociado al calentamiento global del Holoceno, provocó el establecimiento gradual de una taiga. Finalmente, el aumento gradual de la temperatura causó un nuevo incremento en la aridez, restableciéndose el matorral mediterráneo que encontramos en Los Ángeles actualmente. La alternancia entre condiciones áridas-abiertas y húmedas-forestales, así cómo a los procesos de tipo "bottom-up" (cascada trófica ascendente) asociados a la extinción de la megafauna de herbívoros del Pleistoceno, o a la competencia interespecífica establecida entre algunas especies limitó la presencia de algunos miembros de determinados grupos funcionales, causando los cambios en el espectro funcional de las diferentes comunidades.

Conclusiones principales

El análisis global de los resultados nos permitió concluir que las comunidades de mamíferos son entidades dinámicas con una estructura jerárquica que se puede descomponer en partes de menor rango, desvelando nuevas características del sistema en el que se integran. Además, el estudio de las faunas de mamíferos representadas en el registro fósil nos aporta una perspectiva temporal acerca del proceso de estructuración asociado a la formación de las comunidades. Finalmente, el análisis de la estructura de la comunidad de las faunas de mamíferos se confirma como herramienta de inferencia climática útil, resultando de gran utilidad en estudios de tipo paleoecológico y paleoambiental.

ABSTRACT

Title: Influence of global environmental changes on the community structure of Neogene-Quaternary mammalian faunas

Introduction

The main goal of this thesis was to determine how variations on climate have an effect on the community structure of global mammalian faunas, which are highly diverse, both taxonomical and ecomorphologicaly. Carnivores (order Carnivora), due to its underrepresentation in the fossil record, have been frequently excluded from palaeoecological and palaeoenvironmental researches. Nevertheless, although they have been usually considered to be highly independent from the environmental constrains, being limited by the availability and behaviour of its prey, the ecomorphological structure of their communities reflect their specialized hunting behaviours, and should be related to the landscape features where the species develop their activities. Therefore, we paid special attention to this group as a particular assemblage within the mammalian community.

In order to analyse the influence of climate on the structure of the mammalian communities, we used both classical and newly developed methodologies of environmental inference.

Synthesis

In chapter 2 we analysed the capacity of cenograms, which are based on the body size distribution of mammal species, to describe the trophic relationships established between predators and their prey in terrestrial mammalian communities. Based on the original ideas exposed by Valverde, we posed two hypotheses: a) a gap in prey size distributions is developed associated to predators pressure on middle sized prey, and b) a new gap in predators body size distribution is secondarily developed associated to predators pursue towards prey new sizes (“arms race” effect).

We used terrestrial mammalian faunal data from 100 modern localities uniformly distributed throughout the world, excluding Australia, in order to study its cenogram structure. We calculated the magnitude of both, predator and prey gaps, together with the mean body sizes of the different trophic groups. By means of simple linear regressions, we established a relationship between prey's gap magnitude and predators' mean body size, and between predator and prey gap magnitudes. Afterwards, we analysed how the environment influenced the body size structure of the studied communities, by including multiple climatic variables describing the climate of the localities. We, then, performed subsequent stepwise regression analyses including both, climatic and size variables. Finally, we repeated all statistical analyses at two different scales, globally and separating the localities in temperate and tropical ones (latitudinal scale).

Our results showed a statistically significant, but weak, relationship between the continuity in prey body size distribution and the mean body size of predators at both, global and latitudinal scale, which is controlled by environmental factors such as temperature and seasonality. On the other hand, there was no significant relationship at any scale between predator and prey body size distributions associated to the arms race effect. Finally, we only detected a relationship between climatic features, mainly temperature, and the development of a gap in the predator size structure in tropical environments.

According to our results, we are able to reject Valverde's original hypotheses. We failed to find an evolutionary relationship related to the arms race process between predator and prey body size distributions. Predator and prey body size community structures are, otherwise, climatically controlled by the temperature and seasonality of the environment.

In chapter 3 we studied how the community structure, based on cenograms and body size spectra, of the Aragonian faunas from the Madrid Basin (Iberian Peninsula) changed in association with the climatic changes of the middle Miocene. We compared the community structure of six fossil sites from the Madrid basin: Estación Imperial, Paseo de las Acacias, Arroyo del Olivar-Puente de Vallecas complex, Somosaguas, Paracuellos 5 and Paracuellos 3. We used the comparative climatic and faunal data from 100 modern localities and by means of multivariate discriminant analysis, we related their environmental features (type of biome) with the body size structure of their prey communities, taking into account their different biogeographic histories.

Our results showed a dominance of warm and semiarid environments reflected on the structure of the Aragonian mammal associations from the Madrid Basin. Nevertheless, we also detected several pulses of aridity. At the beginning of the sequence, an arid/semiarid and scarcely forested environment was detected, followed by a environmental change to relatively more humid and wooded conditions. Coinciding with the middle Miocene Global Cooling Event, the arid and relatively open conditions reappeared. Finally, relatively more humid and forested landscapes returned during the late Aragonian.

In chapter 4, in order to analyse the community structure of carnivore fossil lagerstätte, in which the herbivores are usually scarce, we developed a new methodology of environmental inference. The carnivore functional groups (CFG) use the body size, dietary and locomotor behaviour of the carnivore species of a community to describe its structure and determine the existence of a statistical relationship with climate.

We gathered all terrestrial carnivores belonging to order Carnivora (250 species) in 11 groups through cluster analysis. The dietary and locomotor behaviours, due to its determining relationship to the energy balance of the species, resulted as the most influential factors in the clustering process. Afterwards, we established the functional structure of the carnivore faunas from 100 modern localities (the same included in chapter 2), as the functional spectrum of each community (meaning the percentage of species belonging to every group). Subsequently, using ANOVA tests, we searched for the bioclimatic signal present in every functional group, but according to these analyses none of the functional groups specifically characterized any particular biome. Therefore, we performed multivariate discriminant analyses, in order to define the relationships between the climate (type of biome) and the functional spectra of the predator communities. In order to consider the climatic and geologic history of the different regions, we repeated these analyses separating the localities into biogeographic realms. Our results exposed the relevance of biogeographic history in the biome discrimination, determining the structuring process of the mammalian communities. Finally, we concluded that different factors control the structural patterns of the communities in temperate and tropical regions. While Pleistocene glaciations, together with physical barriers, constrain the carnivore community structure in Holarctic communities, in tropical realms it is strongly influenced by the high diversity found in these latitudes.

In chapter 5, we finally applied the carnivore functional groups methodology to the carnivore faunas from La Brea Tar Pits, located in Los Angeles, California, in order to analysed how the Late Pleistocene and Holocene climatic changes associated to the glacial-interglacial oscillations, together with the Holocene warming, shaped the structure of the carnivore communities from south-western North American south-western carnivore communities during the last 30,000 years. We compared the carnivore functional spectra of several faunal complexes found in La Brea Tar Pits (California, United States), together with and the one found in Los Angeles today.

Using morphofunctional analyses, we firstly determined the ecological features (diet, locomotion and body size) of the carnivore species found in the different pits. Afterwards, applying discriminant analysis, every species was assigned to a particular functional group, which allowed us to define the functional spectra of every fossil

site. Finally, by means of discriminant analyses, we compared the carnivore functional structure of the different pits with those found in modern Nearctic communities, allowing us to infer the climate (type of biome) for the fossil sites.

The structure variations between the different carnivore communities showed how, during the last 30,000 years, two global climatic shifts modified the south-western landscape in North America. Initially, the arid conditions imposed by the Pleistocene glaciations allowed the development of a sclerophyllous woodland-shrubland, which was gradually replaced by a boreal forest (taiga) due to the increase in the humidity and temperature associated to the Holocene warming. Finally, the rising temperature caused a new increase in the aridity of the environment, and the reestablishment of the sclerophyllous shrubland found in Los Angeles today. The fluctuation between open-arid and forested-humid conditions, bottom-up ecological processes probably caused by megaprey extinctions, and the interspecific competition between some species, limited the presence of some members of certain functional groups, causing the observed modifications of the functional spectra.

Main conclusions

The global analysis of our results indicates that mammalian communities are dynamic entities with a hierarchical structure, which allows us to analyse their smaller units from new points of view. These new analyses reveal new characteristics of the system that are imperceptible at higher scales of analysis. Additionally, the study of the mammalian fossil record gives us a temporal perspective about the assembling processes associated to the community structure. Finally, the mammalian community structure appears reinforced as a good proxy for climatic inference methodologies in palaeoecological studies.

1. INTRODUCCIÓN.

Los mamíferos

La clase Mammalia, actualmente constituida por aproximadamente 5000 especies pertenecientes a 29 ordenes diferentes (Wilson & Reeder 2005), incluye tanto monotremas, como a mamíferos placentados y marsupiales (Wilson 2009). El ser humano, como miembro del mismo, siempre ha mostrado un interés especial por este grupo. Ya sea como fuente de alimento, como potenciales competidores o empleados para llevar a cabo los trabajos físicos que nosotros no podemos realizar, los mamíferos han resultado básicos en el desarrollo de nuestra propia historia (Diamond 1997, Vrba & Schaller 2000). Es más, su amplia representación en las multitud de manifestaciones culturales, artísticas o religiosas muestran la gran influencia de este grupo en nuestro desarrollo. Fue la domesticación de diversas especies lo que nos permitió, en gran medida, pasar de nómadas al sedentarismo, al aportar una fuente de alimento permanente y no estacional, evitando los peligros que la caza entrañaba. Una vez domesticados, los mamíferos pasaron a formar parte del engranaje económico de la sociedad (ganadería, ocio, ecoturismo, etc.), convirtiéndose en el motor económico de algunos países (Honey 1999).

Sin embargo, esta dependencia y competencia directas han tenido, en muchos casos, efectos negativos sobre las faunas de mamíferos de todo el planeta. Ya Ernest P. Walker (1964), apuntaba en su dedicatoria que los “mamíferos, grandes y pequeños, que contribuyen en gran medida al bienestar y la felicidad del hombre, reciben muy poco a cambio, excepto reproches, abusos y exterminación”. Tratados como meras herramientas o animales de compañía en el mejor de los casos, o como alimañas a erradicar en el peor, siempre se los ha considerado elementos ajenos al ambiente que los (y nos) rodea. Por tanto, su explotación, e incluso su exterminio, no tenía efecto alguno sobre el medio. Sin embargo, como miembros de los ecosistemas en los que habitan, su influencia sobre la estabilidad de dichos ambientes queda fuera de toda duda. Numerosos son los ejemplos de las devastadoras consecuencias que han tenido determinadas acciones humanas, como la introducción de especies invasoras en ciertas regiones o el exterminio parcial o total de determinadas especies, sobre el medio (Courchamp *et al.* 2003, Lowe *et al*. 2004, Salo *et al.* 2007, Bergstrom *et al.* 2009, Medina *et al.* 2014). No obstante, y gracias en gran medida a los esfuerzos gubernamentales de los planes conservacionistas (Tanentzap *et al.* 2009, Buckelew *et al*. 2011, Gormley *et al.* 2012) y el aumento de los estudios científicos que centran su interés en los mamíferos, también hay ejemplos de recuperación de ecosistemas en peligro, en los que los mamíferos desarrollan un papel básico (Wallach *et al.* 2010, Sheehy & Lawton 2014).

El registro fósil de los mamíferos comienza en el Triásico medio, periodo en el que coexistieron con los dinosauros. Aunque recientes descubrimientos han mostrado que podían alcanzar tallas significativas (Hu et al 2005; Krause et al. 2014; Well 2014), en general se trataba de animales de pequeño tamaño, pero adaptados a gran variedad de nichos y ambientes. En el límite Cretácico-Terciario, la extinción de los dinosaurios no avianos permitió su diversificación hacia tallas mayores, llegando a encontrarse algunos de sus representantes entre los organismos no coloniales más grandes del registro fósil. Los mamíferos han colonizado tierra, mar y aire, ocupando actualmente todas las regiones del planeta, desde el ecuador hasta los polos. Podemos encontrar especies insectívoras voladoras de menos de 2 gramos de peso, como el murciélago abejorro (*Craseonycteris thonglongyai*), o mamíferos marinos de más de 190 toneladas, como la ballena azul (*Balaenoptera musculus*), cuya principal fuente de alimento es el krill. En los ambientes continentales, los mamíferos son los vertebrados dominantes, llegando a ocupar la mayoría de los nichos disponibles. Además, constituyen una comunidad independiente en el conjunto de comunidades de vertebrados terrestres (Valverde 1967). Como ya mencionáramos antes, en la actualidad se reconocen 3 grandes grupos, Prototheria (monotremas), Metatheria (marsupiales) y Eutheria (mamíferos placentados), en los que se incluyen todas las especies de mamíferos conocidos. Mientras que los miembros de Prototheria y Metatheria están actualmente confinados a los continentes australiano y americano, las especies pertenecientes a Eutheria se encuentran en la práctica totalidad del planeta. Sin embargo, en nuestro trabajo nos centraremos en una división trófica y no exclusivamente cladística del grupo, separando las especies en predadores y presas. Así consideramos predadores a todos los miembros del orden Carnívora, y presas a las especies del resto de órdenes de mamíferos terrestres. Esta separación, si bien simplifica la variabilidad ecológica que encontramos en el medio natural, permite realizar inferencias ecológicas y climáticas a gran escala, facultándonos para comparar comunidades de mamíferos distanciadas en el tiempo y el espacio. Dentro de los distintos órdenes de mamíferos terrestres, en esta tesis mostraremos un interés especial por el grupo de los carnívoros placentados (orden Carnivora).

Los carnívoros placentados se encuentran entre el grupo de mamíferos con mayor capacidad dispersiva, ocupando todas las regiones del planeta a excepción de Oceanía, donde son los carnívoros marsupiales los que ejercen el rol de predadores entre los mamíferos, y la Antártida. Como predadores, dependen en gran medida de la disponibilidad de presas. En consecuencia, se los ha considerado animales con relativa independencia del medio en el que habitaban. Así, un cambio ambiental que provocara el paso de unas condiciones forestales a unas más abiertas no debería suponer un gran problema para estos predadores, dado que la presencia de nuevas presas adaptadas a las nuevas condiciones podría suplir las carencias generadas por la desaparición de sus presas habituales. Debido a esta supuesta independencia del medio en el que habitan, junto con la escasez de restos fósiles hallados en los yacimientos, el grupo de los carnívoros es uno de los grandes olvidados en los estudios paleoambientales y de inferencia paleoclimática. Este hecho viene condicionado por la menor diversidad y abundancia del grupo en el medio natural respecto al de las presas. Generalmente, los trabajos de inferencia paleoecológica basan sus estudios en las faunas de presas presentes en un determinado yacimiento, o estudian su comunidad de mamíferos al completo, donde la influencia relativa de los carnívoros es escasa (Weerd & Daams 1978, Andrews *et al.* 1979, Daams & Meulen 1984, Legendre 1986, Sesé 1991, Meulen & Daams 1992, Montuire 1996, Kay & Madden, 1997, Montuire 1997, Hernández Fernández *et al*. 2006, Domingo *et al*. 2009, García Yelo *et al*. 2014). Sin embargo, existen yacimientos en los que la proporción de herbívoros ***vs***. carnívoros se invierte, y resulta complicado aplicar las metodologías clásicas de inferencia ambiental basadas en las faunas de herbívoros. Podemos encontrar numerosos ejemplos de yacimientos en los que la concentración de restos de carnívoros supera con creces la de herbívoros, como son los cubiles de hienas o las oseras. Dos de los ejemplos más notables son Rancho La Brea (California, EEUU) o, dentro de nuestras fronteras, yacimientos como los del Cerro de los Batallones (Madrid). En estos casos, el desarrollo de nuevas metodologías, que permitan realizar inferencias climáticas y ambientales, puede ayudarnos a comprender mejor cómo los eventos climáticos acaecidos en el pasado han ayudado a estructurar las faunas de mamíferos hasta su situación actual.

Dentro del orden Carnivora, la variabilidad morfológica que encontramos en las distintas especies de carnívoros es un reflejo de la variabilidad dietaría y locomotriz que encontramos dentro del grupo (Van Valkenburgh 1985, 1987, 1988, 1989, Taylor 1989, Friscia *et al.* 2006). Encontramos especies de muy variado tamaño, desde pequeños carnívoros de unos pocos gramos (como la comadreja o *Mustela nivalis*), hasta enormes predadores de varios cientos de kilos (como el oso polar o *Ursus marítimus*). Tanto su dieta, como su locomoción reflejan también esta alta variabilidad. Encontramos ejemplos de especies cuya dieta no es estrictamente carnívora llegando, en algunos casos, a ser eminentemente herbívora; o podemos ver desde especies principalmente arbóreas, que desarrollan sus actividades en los árboles, a especies corredoras, capaces de ejecutar una carrera sostenida durante varios segundos en pro de la persecución de una potencial presa, pasando por especies acuáticas o excavadoras. Es precisamente su alto grado de especialización nos anima a explorar qué efectos, si los tiene, generan los cambios ambientales en las faunas de carnívoros

Finalmente, la amplia diversidad de los mamíferos en su conjunto, tanto taxonómica como ecomorfológica, permite su estudio desde muy diversas disciplinas. Entre las investigaciones más recientes, encontramos trabajos sobre biología evolutiva y del desarrollo (Clauss *et al.* 2014), biogeografía (Leigh *et al.* 2014), paleontología (Woodburne *et al.* 2014), biología molecular (Meyer *et al.* 2014) o ecología (Ripple *et al.* 2014), aunque la mayoría de ellos presentan una temática interdisciplinar. En nuestro trabajo hemos adoptado un enfoque sinecológico, estudiando las faunas de mamíferos en su conjunto y analizando particularmente la estructura de su comunidad.

Estructura de las comunidades

En ecología, una comunidad se define como un conjunto de individuos que habitan un mismo lugar y en un mismo momento, y que interactúan entre sí (Margalef 1977, Krebs 1978, Brewer 1994, Brown 1995, Allen 1998, Begon *et al.* 2006). Así, el estudio de dicha interacción, o Sinecología, analiza las relaciones que estructuran las diferentes comunidades bióticas.

Del mismo modo, una comunidad constituye sistema biológico complejo (Blondel 1986) que posee propiedades comunes, y de rango superior, a todos sus componentes. A medida que su complejidad aumenta, van estableciéndose nuevas interacciones entre los componentes de dicha comunidad (Brewer 1994), produciéndose paralelamente la aparición de nuevas funciones descriptivas de dicha comunidad (Odum, 1971). Su composición específica, la diversidad y dominancia, su biomasa y productividad, su estructura espacial, temporal y trófica o su organización gremial son características que ayudan a describir la estructura de una comunidad (Brewer 1994, Begon *et al.* 2006).

Sin embargo, en los estudios sinecológicos, una de las mayores complicaciones estriba en la definición del propio objeto de estudio, la comunidad. La movilidad de sus componentes hace que el cambio en la composición específica sea gradual (Allen 1998), por lo que definir los límites que separan dos comunidades es complicado y depende, en gran medida, del criterio del investigador (Brown 1995). En nuestro caso, centrándonos en las comunidades de mamíferos, hemos seguido los criterios empleados por Hernández Fernández (2001), que pasamos a exponer a continuación.

En primer lugar seleccionamos 100 localidades distribuidas por todo el planeta según su pertenencia a uno de los diez biomas descritos por Walter (1970). El área de muestreo de cada localidad es de 10.000 km^2 (100x100 Km), limitando la altitud máxima de las localidades a 1000 m. Así, evitamos las variaciones climáticas y faunísticas asociadas a los diferentes pisos altitudinales, pero consideramos todos los posibles tipos de hábitats presentes en cada región (O'Brian 1993).

Cada localidad presenta una comunidad asociada; para determinar la pertenencia de una determinada especie a cada comunidad, se solapa el mapa de distribución de dicha especie con el área geográfica de la localidad en la que se encuentra la comunidad en cuestión. Por último, especificar que, mientras que las especies introducidas por el hombre se han eliminado de los listados, aquellas especies recientemente extintas como consecuencia de la actividad humana se han mantenido en los mismos. En el contexto de los estudios paleoecológicos, las metacomunidades resultan de especial importancia para vincular las múltiples escalas de organización espacio-temporales de las asociaciones biológicas (Leibold et al. 2004). El concepto metacomunidad puede ser definido como el conjunto de comunidades formadas por la unión de múltiples especies geográficamente dispersas que potencialmente son susceptibles de interactuar entre ellas (Wilson 1992). Así, la extrapolación de este concepto a una escala temporal amplia, permite abordar estudios de inferencia paleoambiental a partir de las faunas presentes en los yacimientos paleontológicos, consideradas como comunidades promedio de los diferentes taxones fosilizados a lo largo del tiempo en los yacimientos.

Descriptores de la estructura de las comunidades

Un aspecto fundamental de las comunidades de mamíferos viene dado por la transferencia de materia y energía dentro del sistema o comunidad. En el reino animal, esta transferencia se traduce en la diferenciación de dos grupos tróficos fundamentales, correspondientes a predadores y presas. Así, la transferencia de energía en el sistema puede estar regulada por procesos de tipo "*bottom-up*" (cascada trófica ascendente), cuando son los organismos productores los que controlan el desarrollo de aquellos que se encuentran en la parte superior de la pirámide trófica, o por procesos de tipo "*top-down*" (cascada trófica descendente), cuando son los predadores los que controlan a la población de presas. Se trata, por tanto, de una correlación de fuerzas dinámicas permanente activas, que mantienen los sistemas ecológicos en equilibrio, y que condiciona diversas características biológicas los miembros de una comunidad, definiendo su estructura (Estes *et al.* 1998, Springer *et al*. 2003, Fey *et al*. 2008, Letnic *et al*. 2013, Sandom *et al*. 2013). En este sistema trófico, el tamaño corporal es una de las variables que mayor influencia tiene el la biología de las especies y, por tanto, determina la estructura de las comunidades en mayor grado. En el caso de los predadores, otras dos características biológicas condicionan también la ecología de las diferentes especies, la dieta y tipo de locomoción.

- El tamaño corporal

Ya desde que Huxley (1932) subrayara la relevancia del tamaño corporal como factor ecológico estructural, numerosos trabajos han establecido la importancia del mismo como factor condicionante en gran variedad de características biológicas de los mamíferos (Damuth 1981, 1987, Peters & Wassenberg 1983, McNab 1989, Eisenberg 1990). Así, el tamaño corporal escala con características biológicas básicas de las especies, como son la tasa metabólica, el desarrollo ontogenético, la densidad poblacional o la diversidad específica de una comunidad. Condiciona incluso su tipo de dieta y locomoción, convirtiéndose así en un característica ecológica determinante de primer orden en el desarrollo y comportamiento de los organismos.

- La dieta

En el caso de los mamíferos, la única fuente de obtención de la energía necesaria para realizar todas sus funciones vitales es el consumo de otros organismos. Es el tipo de dieta lo que condiciona su separación en dos grupos tróficos. En general, se considera un predador a toda especie que se alimenta de las otras especies de vertebrados, siendo presa cualquier especie depredada, y cuya dieta se basa, generalmente, en el consumo de los productores primarios (plantas) o insectos. Sin embargo, esta división no puede aplicarse de forma estricta en el medio natural. En el caso particular de los mamíferos, en ambos grupos tróficos encontramos excepciones. Así, dentro del grupo de presas se incluyen habitualmente especies como el chimpancé (*Pan troglodytes*) o el jabalí (*Sus scrofa*), pese a que presentan una dieta eminentemente omnívora que suele incluir pequeños vertebrados, y dentro del de los predadores incluimos especies eminentemente omnívoras, como el kinkajou (*Potos flavus*), e incluso completamente herbívoras, como el panda rojo (*Ailurus fulgens*). Por tanto, es importante especificar que esta división, aunque eminentemente trófica, no sólo sigue criterios dietarios, sino que también suele tener en cuenta la taxonomía de los grupos. En nuestro caso, como ya especificáramos

Figure 1.1. *En esta figura se muestran dos ejemplos de la variabilidad ecológica que encontramos dentro del orde Carnívora. En la parte izquierda de la imagen vemos a un carnívoro mediano, escansorio y con una dieta omnívora, el panda rojo (Ailurus fulgens), típico de los bosques de Nepal, Bhutan y el sur de China. En la parte derecha, observamos un guepardo (Acinonyx jubatus), un gran hipercarnívoro cursorial habitual en las sabanas y desiertos africanos.*

antes, consideraremos predadores a todos los miembros del orden Carnívora, y presas al resto de órdenes de mamíferos terrestres.

- Tipo de Locomoción

La locomoción es uno de los factores ecológicos que mayor gasto energético supone para las especies homeotermas terrestres (Taylor *et al.* 1982, Heglund & Taylor 1988). En el caso de los carnívoros, está directamente relacionado con el tipo de presa que pueden cazar, condicionando el plan corporal de las especies, ya que estas deben desarrollar adaptaciones morfológicas y de comportamiento específicas para cada tipo de locomoción, que las limita, en cierto grado, para desarrollar otras (Taylor 1989).

Como el resto de características ecológicas de las especies, estos factores están limitados por las condiciones del medio en el que habitan las especies (fig. 1.1). Así, la temperatura, la estacionalidad térmica o hídrica, o el grado de forestalidad de la cubierta vegetal (Badgley & Fox 2000, Jayasekara & Takatsuki 2000, Polly 2010, Louys *et al.* 2011), son factores que condicionan la ecología de las especies (regla de Bergmann, diferencias estacionales en el tipo de dieta, presencia de barreras físicas para el desarrollo de actividades de determinadas especies). Por tanto, es importante estudiar cómo las condiciones medioambientales de los ecosistemas determinan la ecología de los organismos, no sólo a nivel de especie, sino para toda la comunidad, regulando las relaciones que se establecen entre sus miembros y permitiéndonos determinar si existen patrones repetitivos (Begon *et al.* 2006).

Convergencia de comunidades y estudios paleoecológicos clásicos

Los estudios ecológicos permiten realizar observaciones a "microescala" sobre de las relaciones que los organismos establecen entre sí, y con el medio que los rodea durante su periodo vital. No obstante, esta disciplina no permite realizar generalizaciones sobre la evolución de los ecosistemas (Rull 1990, Vrba 1992, 1995). Al incluir la dimensión temporal en nuestros análisis, por el contrario, podemos analizar como los diferentes procesos evolutivos causan cambios en su estructura con el paso del tiempo. Estos procesos evolutivos afectan no sólo a las especies, sino también a las estrategias a las que estas se suscriben. Estas últimas dan lugar a una evolución convergente (Allen 1998) que se da tanto a la escala de las especies como de las comunidades (Blondel 1986). La evolución convergente también provoca que, bajo climas análogos, los ecosistemas de distintos continentes presenten una fisionomía general similar, a pesar de estar formados por especies distintas (Margalef 1977).

Partiendo de la premisa de que el clima impone una serie de hábitats que condicionan la estructura de las comunidades (Walter 1970, Cody & Mooney 1978, Blondel 1986, Currie 1991, Kerr & Packer 1997, Shepherd 1998), generalmente se admite también que el estudio de asociaciones de mamíferos fósiles permite reconocer los factores macroclimáticos imperantes en el pasado (Weerd & Daams 1978, Andrews *et al*. 1979, Artemiou 1984, Bonis *et al*. 1992, Andrews 1995, Nieto & Rodríguez 2003, Hernández Fernández *et al*. 2006).

En Paleoecología, dos de las metodologías clásicas de inferencia ambiental que destacan por su aplicabilidad en estudios paleontológicos son el análisis del espectro de diversidad ecológica (Fleming 1973, Andrews *et al*. 1979) y los cenogramas (Valverde 1964, 1967, Legendre 1986, 1989). Estas aproximaciones metodológicas emplean, entre otras características de la comunidad, la distribución de tallas de las comunidades de mamíferos para analizar el tipo de relaciones ecológicas que se establecen entre los miembros de dicha comunidad y de estos con el medio que los rodea.

Espectros de diversidad ecológica

En su trabajo, Andrews *et al*. (1979) desarrollaron el concepto de diversidad ecológica de las comunidades de mamíferos (Fleming 1973). Esta metodología trata de determinar cómo la variabilidad ambiental asociada al gradiente latitudinal y topográfico causa cambios estructurales en las comunidades de mamíferos, al condicionar las adaptaciones ecológicas de sus especies. Entre las adaptaciones que analizaron se encuentran el tipo de dieta, la locomoción y el espectro de tamaños corporales. Concluyeron que, comunidades situadas en regiones cercanas pero con una alta variabilidad climática, pese a compartir un elevado número de especies, presentan una estructura de diversidad ecológica muy dispar. Sin embargo, comunidades situadas en regiones distantes, pero con condiciones ambientales análogas, muestran estructuras de diversidad ecológica similares.

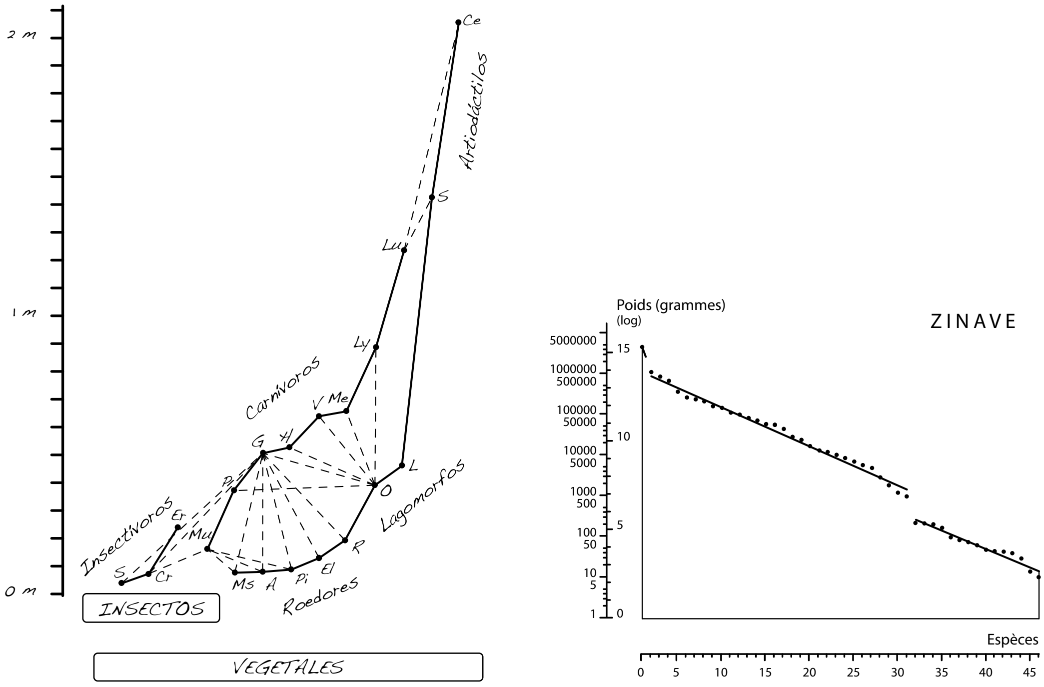
Una vez establecidos los patrones estructurales asociados a los distintos hábitats considerados en su trabajo, compararon la estructura ecológica de la comunidad de mamíferos presentes en 5 yacimientos fósiles del Mioceno y Pleistoceno africanos con los de las comunidades actuales, encontrando paralelismos entre la estructura ecológica de varios yacimientos y ciertas comunidades actuales. La utilidad de esta metodología como herramienta de inferencia ambiental ha hecho de ella uno de los principales métodos para determinar el tipo de ambiente imperante en épocas pasadas (Van Couvering 1980, Nesbit Evans *et al.* 1981, Gaur & Chopra 1983, Collinson

& Hooker 187, Reed 1997, Andrews & O'Brian 2000, Hernández Fernández *et al.* 2006, García Yelo *et al.* 2014).

Cenogramas

Desarrollados por Valverde (1964, 1967), los cenogramas permiten visualizar las relaciones que se establecen entre los miembros de los dos grupos tróficos (predadores y presas) de una comunidad, según su distribución de tallas (peso corporal). Usando la fauna presente en la localidad de Doñana (Andalucía, España), Valverde construyó el cenograma de su comunidad (fig. 1.2) y lo comparó con los construidos para los mamíferos terrestres de Europa y Norteamérica, permitiéndole hacer una serie de observaciones.

1. Existe un "desplazamiento de los fitófagos de las tallas medias" asociado a la presión que ejercen los predadores sobre las especies de tamaño medio. Valverde definió así la banda de predación absoluta como la "zona arriba



Cenograma Valverde

Cenograma Legendre

Figure 1.2. *Modelos originales de cenogramas definidos por Valverde (1967) y Legendre (1987).*

y debajo de la talla media de los predadores donde no existen fit6fagos terrestres" (presas) (Valverde 1967, pag. 197), presente en cualquier cenograma en el que se representen tanto presas como predadores.

2. Los predadores se dividen en dos grupos, macro- y micropredadores, según el tamaño de sus potenciales presas sea mayor o menor que el suyo. Las presas, por su parte, también se separan en dos categorías, macro y micropresas, según su posición en el cenograma quede por debajo o por encima de la banda de predación absoluta.
3. Por último, los predadores modifican su tamaño al perseguir a las presas hacia los extremos de la distribución, produciéndose un desplazamiento secundario en la distribución de tallas de los predadores.

Posteriormente, a partir del trabajo desarrollado por Valverde (1964, 1967), Legendre (1986, 1989) estableció una relación entre el tipo de clima imperante en una localidad y el cenograma de su comunidad de mamíferos. En este caso excluyó del análisis tanto a los quirópteros como a los carnívoros (fig. 1.2). El análisis visual de estos cenogramas le permitió establecer una serie de reglas empíricas.

1. Asoció la presencia de un salto (gap) en la distribución de los pesos de las especies de tamaño medio (500 g a 8 kg) con el grado de forestalidad del ambiente. Así, la presencia de dicho salto (o gap) indicaba ambientes abiertos, mientras que una distribución más continua sugería ambientes más cerrados.
2. Estableció una relación entre la pendiente de la recta de regresión de los pesos de los grandes herbívoros (macropresas) con el grado de aridez del medio. Cuanto mayor era la pendiente, más árido era el ambiente.
3. Por último, estableció una relación inversa entre la pendiente de la recta definida por las micropresas y la temperatura media del ambiente en el que estas habitan.

Numerosos autores han inferido los ambientes imperantes en el pasado a partir del estudio de los cenogramas de la comunidades de mamíferos presentes en los yacimientos objeto del estudio (Morgan *et al.* 1995, Montuire 1998, Storer 2003, Palombo & Giovinazzo 2006, Costeur *et al.* 2007). Sin embargo, debido al carácter visual del análisis otros autores han puesto en duda la utilidad de esta metodología para hacer inferencias paleoambientales (Rodríguez 1999, Croft 2001, Nieto & Rodríguez 2003). Rodríguez (1999) analizó la robustez de los cenogramas como herramienta de inferencia paleoclimática mediante el análisis estadístico de un elevado número de localidades repartidas por todo el planeta. Sin embargo, sólo encontró una relación significativa entre el desarrollo del gap y el grado de forestalidad del medio, y sólo para las regiones tropicales del planeta, invalidado el resto de reglas propuestas por Legendre (1986,1989). No obstante, Hernández Fernández *et al.* (2006) apuntaron que, si se realiza el análisis desde un punto de vista cualitativo en vez de cuantitativo, los resultados obtenidos son consistentes, permitiendo realizar inferencias paleoambientales a partir de la distribución de los pesos de las especies fósiles presentes en un yacimiento.

Dado que el peso es una característica ecológica cuantificable en los organismos fósiles (Creighton 1980, Legendre 1989, Damuth & MacFadden 1990), la aplicabilidad de esta metodología en estudios paleoecológicos queda patente. Si bien el uso de los cenogramas como herramientas de inferencia ambiental es indiscutible, su utilidad para describir de la estructura de las comunidades de mamíferos (Rodríguez 1999, Croft 2001, Palombo 2007) está aún por confirmar.

Ecología de las comunidades de carnívoros e inferencia paleoambiental

Pese a la utilidad de las metodologías anteriormente expuestas, en aquellos yacimientos en los que la representatividad de herbívoros (presas) es escasa (fig. 1.3), este tipo de metodologías no son fácilmente aplicables. Es en estos casos en los que el desarrollo de nuevas metodologías centradas en la inferencia a partir de las faunas de carnívoros pueden resultar de utilidad.

Los grupos ecológicos, también denominados grupos funcionales o gremios,

Figura 1.3. *Reconstrucción paleoambiental y paleoecológica de dos yacimientos excepcionales de carnívoros. A la izquierda del yacimiento madrileño de Cerro de los Batallones (Torrejón de Velasco, España), y a la derecha del yacimiento californiano de Rancho la Brea (Los Angeles, Estados Unidos de America). Las ilustraciones son propiedad de M. antón (Cerro de los Batallones) y R. B. Morsfall (Rancho la Brea).*

se han empleado para definir la estructura de la comunidad de diversos grupos de organismos. Trabajos pioneros sobre plantas, pájaros u organismos marinos (Turpaeva 1953, Salt 1957, Root 1967) trataban de describir la estructura de la comunidad de dichos grupos. Partiendo de esta misma idea, trabajos posteriores sobre las comunidades de mamíferos (Andrews *et al.* 1979, Reed 1998, Hernández Fernández *et al.* 2006, Terry *et al.* 2011, Meachen-Samuels *et al.* 2014) han permitido, no sólo describir la estructura de las comunidades de mamíferos actuales, sino también relacionar dicha estructura con el tipo de ambiente imperante en la región donde se sitúan esas comunidades. En estos trabajos, además, se realizaron inferencias paleoecológicas y paleoambientales a partir de las relaciones establecidas entre la estructura de la comunidad de las faunas actuales y el ambiente donde estas habitan. Sin embargo, el uso de comunidades de mamíferos completas, incluyendo predadores y presas, inhabilita estas metodologías para ser aplicadas en aquellas faunas de yacimientos fósiles donde la representatividad de las presas es escasa o nula. Con el objetivo de poder establecer un marco comparativo bajo el que poder realizar inferencias paleoecológicas y paleoambientales con las faunas de carnívoros de esos yacimientos, nos hemos planteado la necesidad de desarrollar una nueva metodología descriptiva de la estructura de las comunidades de carnívoros terrestres actuales, que además sea capaz de detectar la influencia del clima sobre dicha estructura. Este marco de referencia ha de incluir un número suficiente de registros en los que, tanto la variabilidad ambiental, como la geográfica, queden reflejadas (Rodríguez 1997).

Grupos funcionales de carnívoros

Los grupos funcionales de carnívoros (o CFG según sus siglas en inglés), tratan de definir la estructura de las comunidades de carnívoros según la dieta, locomoción y tamaño corporal de las especies que las componen. Esta nueva metodología representa una oportunidad para describir la estructura de las comunidades de mamíferos, y la influencia del clima en esta estructura, sin necesidad de incluir a las presas en el estudio. Al igual que en las metodologías anteriormente mencionadas, la comparación del espectro funcional de distintas comunidades del planeta, ubicadas en diferentes regiones climáticas, puede aportar indicios sobre cómo el los eventos climáticos globales regulan la estructura de las comunidades de carnívoros, definida por tres factores ecológicos de primer orden (dieta, locomoción y tamaño corporal). Por último, y gracias a los diversos trabajos ecomorfológicos que han establecido relaciones significativas entre la morfología esquelética de las especies de carnívoros y su modo de vida (*e.g.* Van Valkenburgh 1985, 1987, 1988, 1989, 1990, Anyonge 1993, MacLeod & Rose 1993, Iwaniuk *et al.* 1999, Egi 2001, Andersson 2004, Sacco & Van Valkenburgh 2004, Friscia *et al.* 2006, Schutz & Guralnick 2007, Polly & MacLeod 2008, Slater & Van Valkenburgh 2009, Figueirido *et al.* 2010), el uso de esta metodología en los estudios de inferencia paleoclimática es posible.

Objetivos del trabajo

Nuestro estudio se enmarca dentro del campo de la macroecología, que se nutre de disciplinas tan dispares como la ecología, la biogeografía, la paleontología o la macroevolución (Brown 1995). Es necesario estudiar las comunidades a escala global y regional, analizando cómo los procesos climáticos e históricos, junto con la dinámica de las especies y sus relaciones filogenéticas, las estructuran. Más concretamente nos centraremos en el estudio de la estructura de las comunidades o sinecología. Además, hemos incluido una segunda dimensión en el análisis, la temporal, tratando de investigar si la estructura de diversas comunidades de mamíferos se ha mantenido a lo largo del tiempo o ha sufrido cambios. En caso de detectar cambios en la estructura de las comunidades a lo largo del tiempo, hemos tratado de determinar cuáles han sido las posibles causas de los mismos.

Así, los objetivos principales de esta investigación pueden agruparse en dos categorías, una metodológica y una aplicada. En primer lugar, examinaremos dos metodologías descriptivas de la estructura de las comunidades de mamíferos terrestres, que nos permiterán determinar cómo se establecen las relaciones entre los diferentes miembros de las comunidades. Además, trataremos de precisar cómo diferentes factores ambientales condicionan estas relaciones, moldeando la estructura de dichas comunidades, y permitiéndonos estudiar la fiabilidad de estas metodologías para inferir ambientes. Una vez alcanzado el objetivo metodológico, pasaremos al aplicado. En este caso se trata de realizar inferencias de tipo paleoclimático, que nos permitirán detectar los posibles cambios ambientales acaecidos en el pasado, llegando a precisar cómo los eventos de cambio climático han influido en los patrones de estructuración que observamos en las comunidades de mamíferos actuales.

En el capítulo 2º se comprobará la validez de las dos hipótesis propuestas por Valverde (1967): 1) la aparición de un salto en la distribución de tamaños corporales de las presas asociado a la presión ejercida por los predadores, y 2) el subsecuente desarrollo de un salto en la distribución de tamaños corporales de los predadores como resultado de la "persecución" hacia las nuevas tallas de las presas. Con dicho objetivo, analizaremos las relaciones establecidas entre varias variables descriptoras de la estructura de tamaños corporales de predadores y presas. Además, trataremos de determinar si los principales factores implicados en dicho proceso son tróficos o ambientales mediante la incluisón de un conjunto de variables climáticas en los análisis.

En el capítulo 3º se analizará la evolución de la estructura de tamaños corporales de las faunas de mamíferos presentes en una serie de yacimientos fósiles del Aragoniense (Mioceno medio) la cuenca de Madrid (España), asociando dicha evolución a los cambios ambientales detectados durante este intervalo temporal, considerando también la diferente historia geológica y ambiental de los continentes. Para ello se emplearán dos metodologías de inferencia paleoclimática clásicas, ambas fundamentadas en el estudio de la distribución de tamaños corporales de las comunidades de mamíferos de los yacimientos considerados. Se trata de los anteriormente mencionados cenogramas y los espectros de diversidad ecológica. En ambos casos, sólo consideraremos en los análisis al conjunto de presas presentes en dichos yacimientos. Además, en el caso de la metodología de Andrews, sólo analizaremos el espectro de diversidad en tamaños corporales, para que los resultados aportados por ambas metodologías sean comparables.

El objetivo principal del 4º capítulo es agrupar las diferentes especies de carnívoros (orden Carnivora) en grupos según sus características ecológicas (dieta, locomoción y tamaño corporal) para, posteriormente, desarrollar una nueva metodología multivariante, Grupos Funcionales de Carnívoros, que nos permitirá describir la estructura de las comunidad es de las faunas de carnívoros terrestres. Además, analizaremos cómo el clima condiciona la estructura funcional de las comunidades de carnívoros, lo que nos permitirá utilizar los GFC como herramienta de inferencia paleoclimática. Investigaremos también si los factores biogeográficos e históricos, íntimamente relacionados con la capacidad de dispersión de las especies, condicionan los patrones bioclimáticos de las comunidades de mamíferos terrestres.

En el 5º capítulo, se aplicará la metodología desarrollada en el capítulo previo para estudiar las variaciones en la estructura funcional de las faunas de carnívoros presentes en los depósitos de asfalto de Rancho La Brea (Los Ángeles, Estados Unidos), y si dichas variaciones reflejan los cambios ambientales asociados a las distintas glaciaciones sufridas durante el Pleistoceno tardío, junto con el posterior calentamiento del Holoceno.

Finalmente, en el apartado de conclusiones, se presenta una síntesis general de los resultados y conclusiones más destacados de la Tesis Doctoral que nos ocupa, junto con la influencia y perspectivas de futuro de los nuevos campos de investigación abiertos en la presente Tesis Doctoral.

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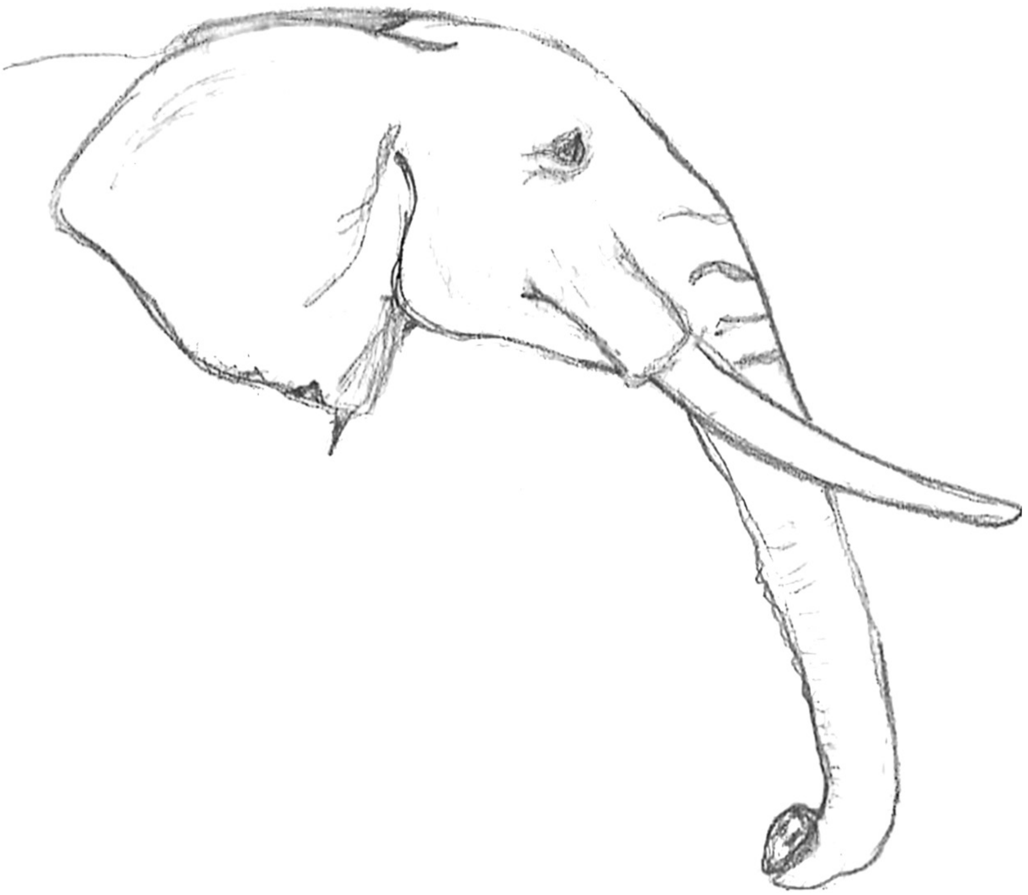

2. PREDATOR-PREY RELATIOSHIPS IN MAMMALIAN COMMUNITIES BASED ON THEIR BODY SIZE STRUCTURE.

Abstract

The analysis of mammalian community structure is a useful tool to understand the relationships between mammal species, as well as their interactions with the surrounding environment. Cenograms describe the body size distribution of mammal communities, revealed as one of the most determining descriptors of the community structure. Valverde's cenograms visually establish the relationship between predator and prey body size structures, expressed as the development of shifts in body size distributions due to the arm race effect. Here, we analysed cenograms of 100 localities uniformly distributed all around the world in order to find out a relationship between the mean body mass of predators and the weight of their prey, as well as to determine the influence of the climate on this relationship. Our results indicate a significant, but weak, relationship between body mass distribution of prey and predators, which is mainly controlled by the temperature and seasonality of the environment. Nevertheless, we failed to establish the expected relationship between predator and prey body size distributions associated to the arm race effect. Instead, the temperature features of the environment are the main controlling factors over predator's body size distribution.

Introduction

Body mass is a biological fundamental factor scaling with several basic features of species and communities as the metabolic rate (Huxley 1932, Kleiber 1932, Misson 1977, McNab 1980, Refinetti 1989, Savage *et al*. 2004, Duncan *et al*. 2007), lifespan/ontogeny (Austad & Fischer 1991, Gillooly *et al*. 2002, Wilkinson & South 2002), locomotion traits (Taylor *et al*. 1982, Garland 1983, Farley *et al*. 1993, Warner *et al*. 2013), dietary constrains (Heglund & Taylor 1988, Nagy *et al*. 1999, Carbone *et al*. 1999), population density (Damuth 1981, 1987, 1991, Fariña 1996, Jennings & Mackinson 2003) or species diversity (Van Valen 1973, Diamond 1975, 1984, Flessa 1975). Additionally, as a structural factor of first order, body mass conditions the relationships among members of the communities, or between them and the environment. Following this idea, several authors developed new methodologies to describe the structure of the mammalian communities by its body size distributions (*e.g*. Foster 1964, Valverde 1964, Van Valen 1965, Andrews *et al*. 1979, Damuth 1981, Brown & Nicoletto 1991, Holling 1992).

Valverde (1964, 1967) visually summarized the body size relationships among the terrestrial mammal species of the community, analysing the trophic interactions established between predators and prey, by plotting rank ordered taxa versus body size in the so-called cenogram (fig. 2.1). Nevertheless, since Legendre (1986, 1989) adapted them to palaeoecological inference, cenograms are more commonly used as a proxy to infer palaeoenvironments through Cenozoic era in all continents (Andrews 1990, Cerling *et al*. 1992, Gunnell 1994, Ducrocq *et al*. 1994, 1995, Auguste 1995, Montuire 1997, 1998, 1999, Arribas & Palqvist 1998, Dashzeveg *et al*. 1998, Wilf *et al*. 1998, Croft 2001, Storer 2003, Costeur 2005, Subamoto *et al*. 2005, Gómez Cano *et al*. 2006, Hernández Fernández *et al*. 2006, Palombo & Giovinazzo 2006, Tougard & Montuire 2006, Costeur *et al*. 2007a, 2007b, Escarguel *et al*. 2008, Becker *et al*. 2009, Deng 2009, Travouillon & Legendre 2009,

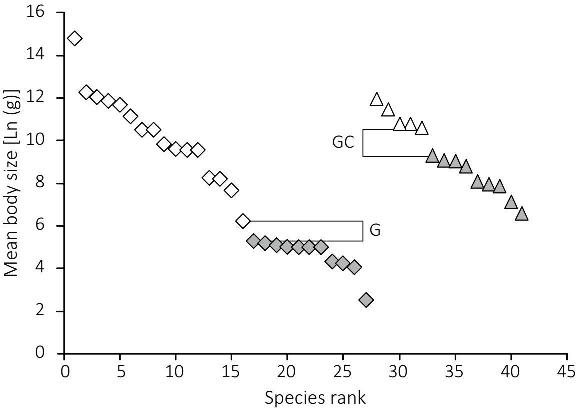

Figure 2.1. *Cenogram associated to the mammal community of Patna (India). Grey diamonds represent small prey, white diamonds represent large prey, grey triangles represent small predators, and white triangles represent large predators. Variables of the cenogram as in table 2.1.*

Travouillon *et al*. 2009, Merceron *et al*. 2012, Lyman 2013, García Yelo *et al*. 2014, Stoetzel *et al*. 2014). Nevertheless, due to the low or null quantitative relationship found between the cenogram variables defined by Legendre and the environment, some other authors recommended use cenograms as originally proposed by Valverde (Rodríguez 1999, Croft 2001, Nieto & Rodríguez 2003), as a tool for the description of the body size community structure of terrestrial mammalian faunas and to elucidate relationships between different guilds, as well as the internal dynamic of the communities. The original eco-evolutionary hypotheses proposed by Valverde, however, have not been tested yet.

In his seminal work, Valverde (1964, 1967) detected the prey displacement from medium sizes (between 0,5 and 8 kg), due to the pressure exerted by predators over the middle-sized prey. Predator's preference on medium-size prey is a consequence of the higher ratio between the energy gained from them and the energy devoted to hunt them (Valverde 1967, Gittleman 1985, Owen-Smith 2002, Radloff & Du Toit 2004, Carbone *et al*. 2007, Owen-Smith & Mills 2008). Additionally, following prey's displacement from medium sizes, predators also move towards larger or smaller sizes, with large predators focusing in large prey and small predators in small prey and giving rise to an "evolutionary arms race" (*sensu* Vermeij 1987). As a consequence of these displacements, two gaps appear in both, predator and prey body size distributions (fig. 2.1).

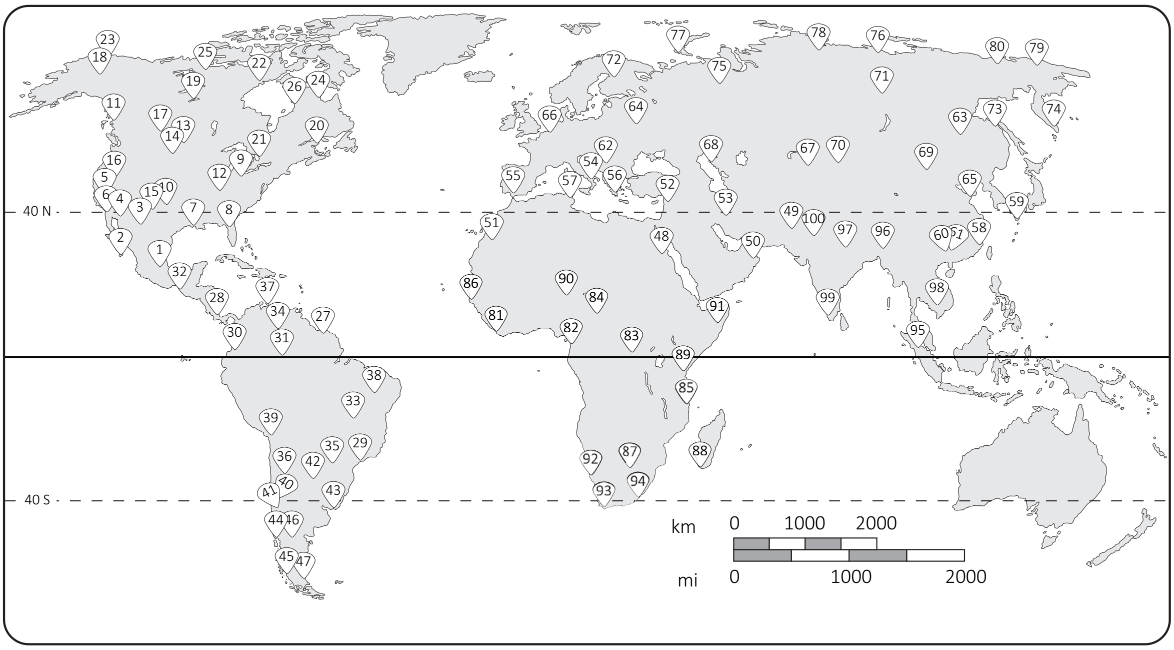

Figure 2.2. *Distribution of the 100 communities studied in this work. The dashed lines separate the tropical and subtropical realm from the temperate ones. Locality numbers as in appendix 1.*

The aim of this research is to test both Valverde's hypotheses: 1) the development of a gap in prey size distributions associated to predators pressure, and 2) the development of a gap in predators body size distribution associated to predators pursue towards prey new sizes. For such a purpose we analysed the relationships among different variables of the body size structure of predators and prey. Furthermore, in order to determine the relevance of environment over such relationships, we also included a set of climatic variables in the analysis. Finally, we also analysed the influence of climate on the relationships, as the environmental histories of the continents determine the faunal composition of different regions through the development of physical and environmental barriers or connections among them, conditioning its mammalian community structure (Simpson 1947, 1950, Hopkins 1959, Webb 1976, Gingerich 1985, Moreno Bofarull *et al*. 2008, Lozhkin *et al*. 2011).

Material and Methods

We used climatic and terrestrial mammal faunal data for 100 modern localities uniformly distributed throughout the world (fig. 2.2; appendix 1). Nevertheless, we excluded Australia from our analyses due to the particular characteristics of its original faunas, exclusively formed by marsupial species and underrepresented in mammal predators (Strahan 1995, Wroe *et al*. 2004). We excluded from the faunal list species introduced by anthropic action, but those species that were extinct in historic times were incorporated to them.

In order to describe the community structure of the mammal fauna present in each locality, we built its cenogram by plotting the rank ordered taxa versus body size (fig. 2.1). Following Valverde (1964), we plotted separated predators (species belonging to the order Carnivora) and prey (species belonging to all the remaining

Variables	Descripción
W3	Mean body weight (mass) of all small preys (< 500 g) (in Ln (g) units)
W1	Mean body weight (mass) of all large preys (≥ 500 g) (in Ln (g) units)
WC1	Mean body weight (mass) of all small predators (< 15 Kg) (in Ln (g) units)
WC3	Mean body weight (mass) of all large predators (≥ 15 Kg) (in Ln (g) units)
WC	Magnitude of the gap between small and large preys (in Ln (g) units)
G	Mean body weight (mass) of all predators presents in the locality (in Ln (g) units
GC	Magnitude of the gap between small and large predators (in Ln (g) units)

Table 2.1. *List of cenogram variables used in our research (fig. 2.1). Modified from Rodríguez (1999) and Hernández Fernández et al. (2006)*

Abb.	Climatic Variable	Unit	References
T	Annual mean temperature	°C	
Tp	Annual positive temperature	0.1 °C	Rivas Martínez (1994)
Tmax	Mean temperature of the warmest month	°C	
Tmin	Mean temperature of the coldest month	°C	
Mta	Mean annual thermal amplitude	°C	Rivas Martínez (1994)
It	Thermicity index	0.1 °C	Rivas Martínez (1994)
Itc	Compensated thermicity index	0.1 °C	Rivas Martínez (1994)
W	Winter length	Months	
VAP	Vegetative activity period	Months	Fernández González (1997)
FVAP	Free vegetative activity period	Months	
Io	Ombrothermic index		Rivas Martínez (1994)
P	Annual total precipitation	mm	
D	Drought length	Months	Walter (1970); Rivas Martínez (1987)

Table 2.2. *List of climatic variables (appendix 1, fig. 2.2) used in this work (following Hernández Fernández & Peláez-Campomanes 2005).*

orders of mammals). Species were then classified according to its body size in four categories: small prey (< 500 g), large prey (≥ 500 g), small predators (< 15 Kg) and large predators (≥ 15 Kg) (modified from Gittleman 1985, Legendre 1986, 1989, Carbone *et al*. 1999). The body size data of each species were obtained from Smith *et al*. (2003). For those few species with no data on body size, most of them small mammals under 5 kg, we calculated the mean body size of their genera (Rodríguez 1999, Croft 2001, Hernández Fernández *et al*. 2006). Once the cenograms were constructed we calculated predator and prey gaps. Prey's gap (G) is the magnitude of the gap between the largest small prey and the smallest large prey, whereas predator's gap (GC) corresponds to the gap between small and large predators (fig. 2.1).

We used both variables, together with the mean body weight of the predators (fig. 2.1, table 2.1), to analyse the existence of evolutionary relationships between the body size structure of predators and their prey in our communities. In order to test how the pressure exerted by predators determines the development of the gap in prey body size distribution, we related, by means of simple linear regression, prey's gap (G) to predators mean body size of (WC). Afterwards, we related GC to prey's gap (G) through simple linear regression to examine whether prey's gap development causes a change in predators body size distribution by triggering predator's gap (GC) development.

We also calculated the mean body sizes of the different categories in predators and prey, in order to visually evaluate how these variables change with gaps development and environmental differences (table 2.1).

Additionally, with the aim of determining the climate influence on the body size structure of the studied communities, we also gathered environmental data on thirteen climatic variables for all the localities (table 2.2). We performed a principal component analysis (PCA) on the climatic variables to reduce its possible collinearity and to simplify the statistical testing of both hypotheses. We then performed subsequent stepwise regression analyses including both, climatic PCA scores and size variables, to test the climatic influence over both hypotheses.

Finally, we repeated the analyses at two scales to determine the possible effects of differences in climatic history during Pleistocene. We first analysed all communities together (global analysis), and secondly we separated them in tropical *vs*. temperate ones (latitudinal analyses). We made the tropical/temperate division based on the biome classification (Walter 1970, Hernández Fernández 2001), with biomes I-III and V classified as tropical, and biomes IV and VI-IX classified as temperate (see appendix 1 and supplementary data 2.1).

	PCA	
	Clim_1	Clim_2
Eigenvalue	8.79	2.57
% of total variance explained	67.61	19.78
Cumulative %	67.61	87.39

Variable	Component matrix	
T	0.993	-0.049
Tp	0.963	-0.049
Tmax	0.868	-0.240
Tmin	0.983	0.044
Mta	-0.865	-0.201
It	0.987	0.022
Itc	0.990	-0.027
W	-0.919	0.026
VAP	0.964	-0.064
FVAP	0.460	0.765
Io	-0.241	0.740
P	0.453	0.819
D	0.450	-0.811

Table 2.3. *Results of the PCA analyses with climate variables for both hypotheses studied in this work. The component matrix shows the correlations between every variable and each of the PCA factors. Abbreviations for variables as in table 2.2.*

Results

Climatic Principal Components Analysis.

The climatic PCA retained two significant components, accounting for about 87% of the variance in the original climatic data (table 2.3). Whereas the first component (Clim_1) reflects the thermal features of the climate, the second one (Clim_2) is related to the hydric characteristics of the environment (mainly drought length and annual total precipitation). Whereas Clim_1 increases when overall temperature increases (mean annual temperature, compensated thermicity index and the vegetative activity period increase) and thermal seasonality decreases, Clim_2 increases when precipitation rate increases and drought length decreases.

		Dep. Var.	Step	p	R^2	B	Indep. Var.
Global		G	1	<0.001	0.246	-0.567	Clim_1
			2	<0.001	0.419	-0.621	Clim_1
						0.812	WC
Latitudinal	Temperate	G	1	<0.001	0.329	-0.873	Clim_1
			2	0.001	0.465	-0.776	Clim_1
						0.799	WC
	Tropical	G	1	0.005	0.154	-1.222	Clim_1
			2	0,001	0.298	-1.336	Clim_1
						0.709	WC

Table 2.4. *Results for the stepwise regression analyses between the magnitude of prey's gap (G) and predators' mean body size (WC) together with the climate principal components for global and latitudinal analyses.*

Arms race effect on the body size structure of mammalian communities.

A statistically significant, but weak, positive relationship exist between the magnitude of prey's gap (G) and the mean body size of predators (WC) at global ($r^2 = 0.107$; $p = 0.001$) and latitudinal scale (tropical: $r^2 = 0.116$, $p = 0.015$; temperate: $r^2 = 0.210$, $p = 0.001$). Nevertheless, these relations are statistical artefacts caused by a few localities from the tropical desert (Arica in Chile) and the tundra (Malye-Karmakuly and Mys Chelyuskin, both in Russia) that polarize the distribution, giving a false significant correlation between G and WC in all analyses (fig. 2.3A). When these localities are removed, no statistical relationship remains (global: $r^2 = 0.002$, $p = 0.632$; tropical: $r^2 = 0.034$, $p = 0.208$; temperate: $r^2 = 0.014$, $p = 0.427$). On the other hand, there is no correlation between the magnitude of predator's gap (GC) and prey's gap (G) at any scale (fig. 2.3A-B).

When we also considered the climatic components results slightly improved, but in a different way for both hypothesis. In the first hypothesis, where we test the effect of predator pressure over prey's body size distribution, results improve at the two climatic scales (table 2.4). In all cases, clim_1 and WC are included in the stepwise regression analyses that calculate the gap in prey distribution (G) but, whereas the thermal features of the climate (clim_1) present a negative correlation with the magnitude of prey's gap (fig. 2.3C), predators mean body size (WC) positively

		Dep. Var.	Step	p	R^2	B	Indep. Var.
Global		GC	-	-	-	-	-
Latitudinal	Temperate	GC	-	-	-	-	-
	Tropical	GC	1	0.014	0.132	-5.282	Clim_1

Table 2.5. *Results for the stepwise regression analyses between the magnitude of predators' gap (GC) and the magnitude of prey's gap (G) together with climate principal components for global and latitudinal analyses.*

correlates with this gap. On the contrary, our results for the second hypothesis indicated that there is no relationship between the development of prey's gap and the change in predator's body size structure, except for the tropical domains in the latitudinal analysis, where thermal features of the climate (clim_1) present a negative relationship ($r^2 = 0.190$, $p = 0.002$) with predator gap's magnitude (table 2.5, fig 2.3D). Although, the tropical desert locality of Mendoza (Argentina, South America) slightly polarizes this relationship, results do not vary significantly when we removed the effect of this locality ($r^2 = 0.132$, $p = 0.014$). Thus, at latitudinal scale, only the climate seems to regulate predator's body size distributions and just for tropical realms of the world.

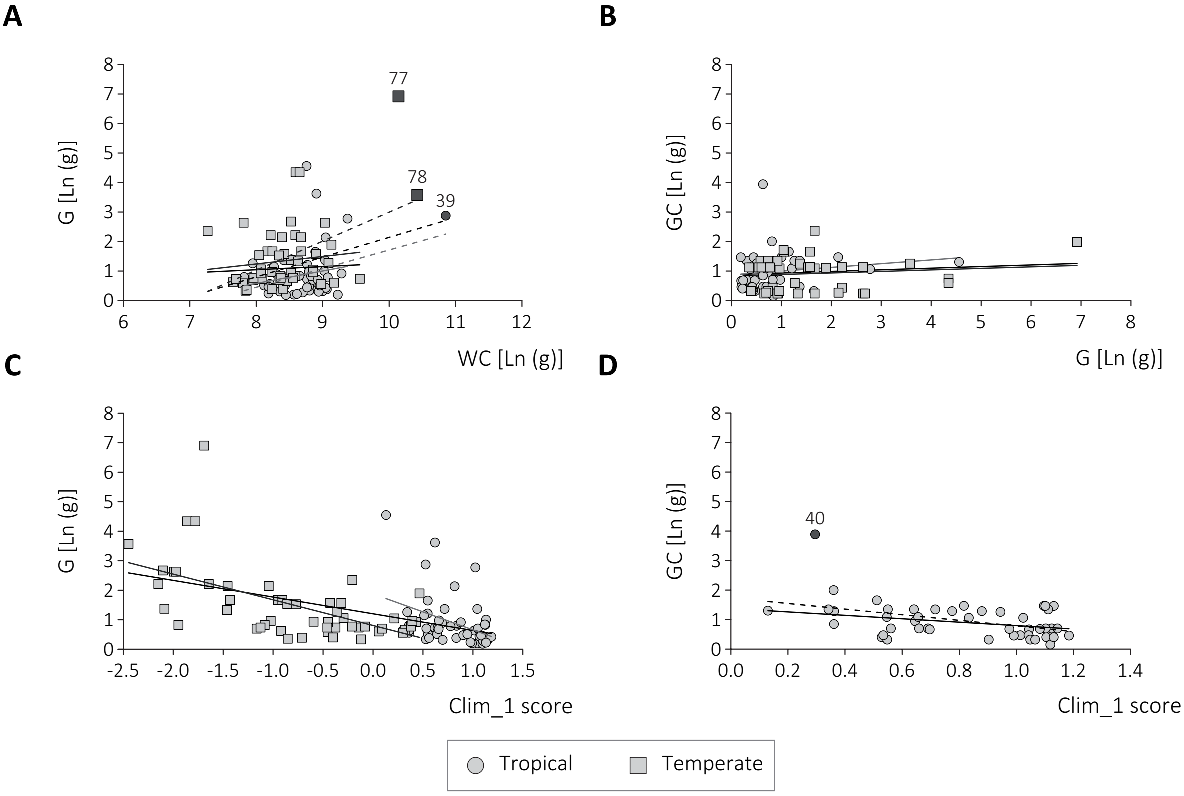

Figure 2.3. *Linear regressions established between: A) the magnitude of prey's gap (G) and predators mean body size (WC); B) predators' and prey's gaps magnitudes (GC and G respectively); C) the magnitude of prey's gap (G) and the first climate principal component (Clim_1); and D) the magnitude of predators gap (GC) and the first climate principal component (Clim_1). Light grey circles and squares represent the tropical and temperate communities respectively. Dark grey circles and squares represent the outliers mentioned in the main text (locality numbers as in appendix S1). Lines represent the regressions at both, global (black line) and latitudinal scales (light grey for the tropical analysis and dark grey for the temperate one). Dashed lines represent the regressions with the outliers included.*

Discussion

Our results show no clear evidence of an arms race between predators and prey at least in terms of changes in their body size distributions. Therefore, we should reject Valverde's hypotheses. Valverde (1964) proposed predator and prey relationship in terms of evolutionary patterns, with prey species changing their body sizes as a consequence of the predator pressure, and the subsequent predator body size changes as a response to prey body size evolution. Nevertheless, our results do not support this evolutionary pattern, since we identified these displacements as a lack of species of these particular body sizes, not as body size changes within lineages. Predator pressure can cause the development of a gap in prey body size distribution around middle sizes, but this relationship is strongly conditioned by the climate, that highly influences prey body size community structure. Additionally, we can point out that there is no relationship between the development of a gap in predators body size distribution and the presence of in middle size gap in prey, not even when climatic features of the environment are taken into account. Predators' body size distribution seems to be ruled by the aridity of the environment, and only in the tropical areas of the world.

Shifts development in predator and prey body size distributions and the Arms races hypothesis.

Valverde's hypotheses are not supported by our results. Predators mean body size does not directly constrain prey body size distribution and, consequently, there is not a side effect on predator community's body sizes due to prey's body size avoidance. Nevertheless, once we consider the climate in our analyses, weak but significant relationships between G, temperature features (Clim_1) and WC at global and latitudinal scale (table 2.4, fig. 2.3C), and a negative one between GC and temperature features for the tropics arise.

Prey's gap (G) is larger in those localities where the environment is cooler, with high thermal seasonality and low vegetative activity period, and where predator community has larger mean body sizes. Prey's gap development can be caused by the absence of large small prey, which reduces the mean body size of small prey guild, or by the lack of small large prey, which increases the size of large prey guild size. In fact, our data indicate that both processes are acting together (fig. 2.4A). While in cold and seasonal environments large prey guild has bigger mean sizes and small prey one are smaller, in warmer and stable localities mean body sizes of both guilds get closer by small prey guild increases of its mean body size ($r^2 = 0.265$,

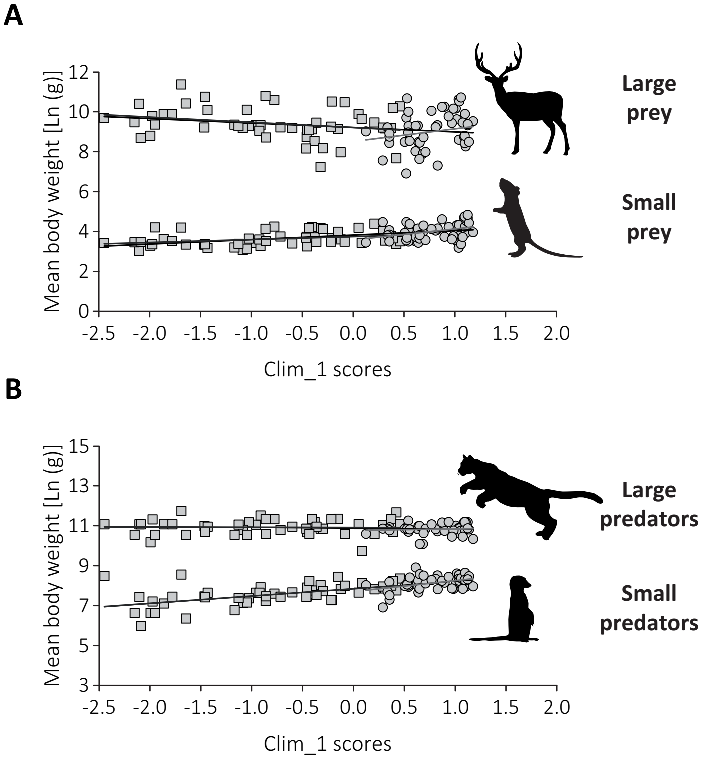

Figure 2.4. *Relationships established between the first climate principal component (Clim_1) and the mean body sizes of the different trophic guilds of prey (A) and predators (B). Cenogram variables named as in table 2.1. Light grey circles and squares represent the tropical and temperate communities respectively. Lines represent the regressions at both, global (black line) and latitudinal scales (light grey for the tropical analysis and dark grey for the temperate one).*

$p < 0.001$) and slight reduction of the large one ($r^2 = 0.051$, $p = 0.024$). The different effect of the temperature over middle-sized prey, mainly browser species with a high metabolic rate, could be related to the lack of specific adaptations to the seasonal availability of resources in temperate climates, which potentiates the negative effect of the herbivorous diet due to the low nutritious quality of vegetation. Plants develop physical mechanisms (as protective structures like thorns or cellulose increase) and chemical defences as a response to consumption by herbivorous prey (McNaughton *et al*. 1985, Cooper & Owen-Smith 1986, Westoby 1989, Du Toit 1990, Milewski *et al*. 1991, Palo & Robbins 1991, Loeuille *et al*. 2002, Rostás *et al*. 2013), mechanisms sometimes potentiated under moderate herbivore pressure (Lindroth & St. Claire 2013), which reduces its nutritional intake. The constraining effect of the low quality of vegetation increases in cooler and seasonal environments due to the seasonal lack of resources. Large herbivores have developed mechanisms allowing them to avoid the problems associated to a diet based on low-quality plants, such as the elongation of the digestive tract, the increase of gut capacity or multiplicity of the stomachs (Jarman 1974, Bell 1969, 1971, Paraa 1978, Owen-Smith 1988, Van Soest 1996, Clauss *et al*. 2003). They also elude scarcity of resources during winter through migrations to different foraging and living areas (Fryxell & Sinclair 1988, Hansen *et al*. 2011, Monteith *et al*. 2011). Small mammals, on the other hand, adopt hoarding behaviours that allow them to store food for the winter season or increasing the amount of energy-rich animals in their diet (Merritt 1986, Schwaibold & Pillay 2006).

Middle-sized prey, however, are not able to completely apply for these defensive resources. Consequently, middle-sized prey seem to be particularly affected by the seasonal availability of plants and the increasing harshness of the environment with decreasing temperature. These results seem to reflect a principal controlling bottom-up effect of the vegetative growth over prey guilds body sizes. Additionally, besides this environmental control of the magnitude of prey's gap, appears to be a very weak top-down effect of predator mean body size over prey body size distribution (table 2.4).

Finally, in large prey this relationship between W3 and the thermal features of the environment is no longer maintained when we separate temperate ($r^2 = 0.067$, $p = 0.071$) and tropical ($r^2 = 0.026$, $p = 0.263$) localities in the latitudinal analysis (fig. 2.4A). Small prey, on the contrary, maintain the same pattern in both, tropical ($r^2 = 0.133$, $p = 0.009$) and temperate ($r^2 = 0.113$, $p = 0.017$) latitudes.

We found no relationship between the magnitude of predator's gap (GC) and any variable at global scale or in temperate regions (table 2.5). Nevertheless, in tropical areas, predator body size distribution seems to be controlled by the temperature (table 2.5), just like in the case of prey body size distribution. For tropical latitudes, the predators' gap is larger in cooler and more seasonal environments, decreasing as temperature increases and thermal seasonality disappears. In warm and stable environments, mainly tropical deciduous forest and evergreen tropical rainforest, the smaller magnitude of the gap in predators is caused by the presence of some species (*Chrysocyon brachiurus*, *Lycaon pictus*, *Pteronura brasiliensis*, *Aonyx capensis*, *A. congicus* or *Neofelis nebulosa*). These species, on the contrary, are absent in the cooler localities of the tropics (mainly temperate evergreen forest and tropical desert), which increase the magnitude of the predator gap of these localities. Their absence seems to be related to the species richness latitudinal gradient (Wallace 1878, Fischer 1960, Pianka 1966, Haffer 1982, Vrba 1995, Collinvaux *et al*. 2000, Hernández Fernández & Vrba 2005, Moreno Bofarull *et al*. 2008). Productivity decreases as the latitude grows, reducing the niche and resources available for mammal species (Currie & Paquin 1987, Currie 1991, Kerr & Packer 1997, Shepherd 1998, Rodríguez *et al*. 2006), and conditioning their presence in those regions. Located in the subtropical range of the tropics, localities from temperate evergreen forests and tropical deserts have lower values in number of species than the tropical forest ones, being impoverished in all guilds (see appendix 1).

Therefore, the increase of the magnitude of the gap in predators is not caused by size changes in both predator guilds, but only in the small one. There is a positive relationship between the mean body size of predators and PCA first factor (Clim_1) for small predators at any scale (global: $r^2 = 0.475$, $p < 0.001$; tropical: $r^2 = 0.185$, p

= 0.002; temperate: $r^2 = 0.295$, $p < 0.001$), whereas this relationship is not significant with larger ones (fig. 2.4B) at both, global ($r^2 = 0.014$, $p = 0.252$) and latitudinal scale (tropical: $r^2 = 0.006$, $p = 0.608$; temperate: $r^2 = 0.001$, $p = 0.868$). As warmer and less seasonal is the environment, larger is the community of small predators that we found, while large predators maintain a similar mean body size over the whole latitudinal gradient. This confirms that change trends in the magnitude of predators' gap are associated to variations in small predators guild.

Climatic effect on small mammals richness in extreme biomes.

A few communities, with low values in predator species richness of our database (appendix 1), polarize our results and establish false relationships between predator and prey body size distribution. These communities are located in the Russian tundra and in the South American deserts and are particularly impoverished in small predators, having just one or two representatives of this size category, most of them heavier than 4 kg. This overrepresentation of large species shoot up predators mean body size (WC) or increase the shift between both predator's guilds (GC).

Malye-Karmakuly and Mys Chelyuskin are some of the driest and/or coldest localities in our database and its small predator guilds have high values in mean body size. Its landscape is dominated by bushy vegetation and partially frozen soils, which mainly supports small insects and migratory or very small herbivores (Chernov 1985, UCMP Team 2013). Consequently, only predators with a carnivorous or hipercarnivorous diet are able to survive in these regions. The positive relationship recently established between body size and carnivory (Carbone *et al*. 1999, 2007), can explain the underrepresentation of smaller predators in some of the driest and coldest regions of the planet, as small predators would find difficult to survive in these localities due to its harsh environment.

The low predator species richness found in South American deserts is a consequence of the particular biogeographic history of this realm. The Great American Biotic Interchange (Simpson 1950, Marshall *et al*. 1982) seriously affected the predator fauna of South America during the late Pliocene. Nevertheless, this faunal exchange was confined to the lower temperate and tropical latitudes and only representatives of few families of carnivores were able to migrate from North to South America, dispersing through the tropical realm (Simpson 1950, Webb 1976). After the extinction of the carnivore marsupials, placental carnivores became the dominant mammalian predators in South America (Simpson 1950, Marshall 1981, Lessa & Fariña 1996, Webb 2006), but only a few species were adapted to desert conditions. While in Arica, the driest locality in our dataset and isolated from the fauna found in nearby biomes by the Andes Mountain range, only the puma (*Puma concolor*) is capable of survive (Moreno Bofarull *et al*. 2008, Sunquist & Sunquist 2009), in Mendoza, one of the coldest desert localities and only slightly less arid than Arica, we only find another species allowed to inhabit, the lesser grisson (*Galictis cuja*). This species, commonly found in evergreen forest and savanna regions nearby Mendoza, is also well adapted to survive in open and arid environments (Mares *et al*. 1989, Yensen & Tarifa 2003) like the tropical desert of Mendoza, being able to survive in this locality.

Finally, in both cases, the tundra and desert localities, also the effect of big predator's pressure over smaller ones would imply the complete absence of the smaller species in those places where larger predators are present (Palomares *et al*. 1995, Fedriani *et al*. 2000, Berger *et al*. 2008, Johnson & VanDerWal 2009, Steinmetz *et al*. 2013)

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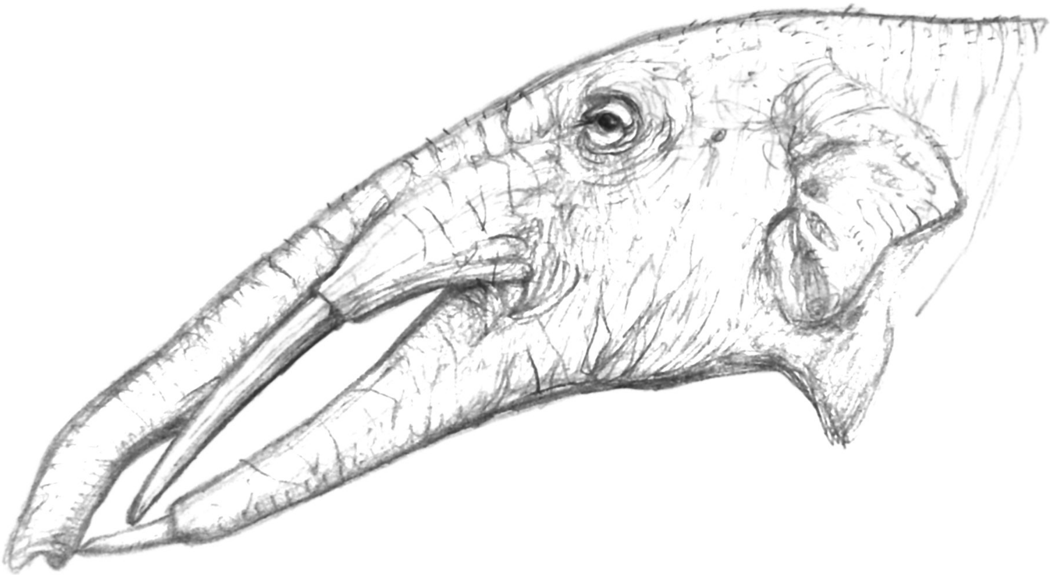
Supplementary data

Supplementary data 2.1. *Climatic typology used in this research (following Walter 1970, Hernández Fernández 2001).*

Biome	Zonobiome (vegetation type)
I	Evergreen tropical rainforest
II	Tropical deciduous woodland
II/III	Savanna
III	Sub-tropical desert
IV	Sclerophyllous woodland-shrubland
V	Temperate evergreen forest
VI	Nemoral broadleaf-deciduous forest
VII	Steppe to cold desert
VIII	Boreal coniferous forest (taiga)
IX	Tundra



3. PALAEOENVIRONMENTAL ANALYSIS OF THE ARAGONIAN (MIDDLE MIOCENE) MAMMALIAN FAUNAS FROM THE MADRID BASIN BASED ON BODY-SIZE STRUCTURE.

Abstract

As a consequence of the growth of the Antarctic ice-sheet during the middle Miocene, a global decrease of temperatures and an associated increase in aridity provoked several environmental changes all around the world. Such environmental variations can be detected in the continental record of the mammalian prey community structure using a synecological approach. Because of the good quality of its faunas, the rich Aragonian vertebrate fossil record from the Madrid Basin (Spain) appears as a good candidate to explore these environmental changes. In order to analyse the climatic evolution of the Iberian Peninsula associated to the Global Cooling Event, two classic palaeo-synecological methodologies (cenograms and body size diversity), based on body-size community structure, were applied to 6 fossil sites from the Madrid Basin, ranging over 2 million years (15.5 – 13.5 Ma). To establish a comparative framework, we used the ecological faunal data from 100 modern localities uniformly distributed all around the world. Our palaeoenvironmental inference is based on multivariate discriminant analysis of the dataset containing both modern and fossil mammals. Finally, we can conclude that the Aragonian mammalian assemblage from the Madrid Basin showed a predominance of semiarid environments with pulses of higher aridity in biozones Dc, E and F associated with the Global Cooling Event of the middle Miocene.

Introduction

The Miocene Climatic Optimum (MCO), recorded ~17 to 15 Ma, represents one of the warmest periods of the last 30 million years (Zachos *et al.* 2001, Shevenell *et al.* 2004). It lasted until 14 Ma, when a climatic change from warm and humid conditions to a more arid and cooler environment took place as a consequence of the growth of the Antarctic ice-sheet. This climatic change, known as Global Cooling Event, has been recorded in both marine and continental records using sedimentary and faunal data (e.g. Kennett & Barker 1990, Böhme 2003, Zachos *et al.* 2001, Lewis *et al.* 2008). Clift (2010) related changes in erosion rates across Eurasia, North America and Africa with climatic fluctuations during the last 33 Ma, peaking around 16 Ma ago. In Hauptvogel and Passchier's (2012) study, the analysis of heavy mineral composition of one drill core allowed them to define the Antarctic ice dynamics related to the climatic change during the early to middle Miocene (17 to 14 Ma). Faunal studies based on the evolution of hypsodonty in large herbivorous mammals from Asia (Liu *et al.* 2008), and modifications on ecophysiological structure of herpetological assemblages (Böhme *et al.* 2010), also detected a significant increase in aridity related to the Global Cooling Event. Finally, Larsson *et al.* (2011) investigated palynological composition of sediments from the Danish coast (lower to upper Miocene, 19 to 8 Ma) that also showed major climatic shifts during the Miocene.

As homeotherms and habitat-sensitive animals, mammals are one of the best proxies to detect these climatic changes in the continental record (Vrba 1992, Barnosky 2001). Variations in their ecological characteristics can be used to detect environmental constraints. In fact, shifts in their feeding habits (Domingo *et al.* 2009, 2012, De Miguel *et al.* 2011, Zhou *et al.* 2011), locomotor adaptations (Lewis 1997, Samuels & Van Valkenburgh 2009, Meloro 2011), and body size or morphology (Legendre 1986, Shepherd 1998, Rodríguez 2001) have been found to correlate to climate and ecological dynamics. Besides, body size has been traditionally related to climate via Bergmann's and Allen's rules (Bergmann 1847, Allen 1877), which stated a latitudinal variation pattern in mammal (and birds) body size and shape. These rules have been almost equally accepted (Mayr 1956, 1963, Ashton *et al.* 2000, Ashton 2001, Meiri & Dayan 2003) and rejected (Scholander 1954, McNab 1971, Fuentes & Jaksić 1979, Meiri *et al.* 2007). Although the original ideas expressed by Bergmann and Allen are not exactly supported, a relationship between climatic proxies and mammal body size can be established (Boyce 1978, Wigginton & Dobson 1999, Yom-Tov & Geffen 2006) and confirms the value of this feature in climate inference.

However, the relationship between mammalian ecology and climate is not only reflected at the individual level, but also in the structure of the communities.

During the last decades, the palaeoclimate from different periods and regions has been established based on the body size community structure of mammal fossils (Legendre 1986, 1989, Montuire 1999, Rodríguez 1999, Croft 2001, Storer 2003, Hernández Fernández *et al*. 2006a, Palombo & Giovinazzo 2006, Tougard & Montuire 2006, Costeur *et al*. 2007, Travouillon & Legendre 2009, Travouillon *et al*. 2009).

The well-studied mammalian groups from the Iberian Peninsula (Meulen & Daams 1992, Fraile *et al*. 2000, Hernández Fernández *et al*. 2003, 2006a, Domingo *et al*. 2009, 2012), among the richest of the Neogene (Daams *et al*. 1977, Alba *et al*. 2001), represent a good opportunity to analyse ecomorphological aspects of fossil assemblages and their relationship to the climatic change that took place ~ 14 Ma ago. Particularly, the evolution of the body size community structure of the middle Miocene prey fauna from the Madrid Basin allows us to explore the connection between ecological community dynamics and macroenvironmental changes.

The Madrid Basin, originated by an endorheic lacustrine system (Calvo 2000), is filled by detrital, evaporitic and carbonatic sediments. The age of the whole section ranges between 20 to 5.4 Ma, with three different lithostratigraphic units from the Madrid Basin defined (Alberdi 1985, Calvo 1989, Calvo *et al*. 1993): the Lower Unit (Ramblian to middle Aragonian), the Middle Unit (middle Aragonian to Vallesian) and the Upper Unit (Vallesian to Turolian). Several similar changes between humid and arid conditions have been also detected in this region for this short time in previous studies about the modifications in mammal body size community structure (Hernández Fernández *et al*. 2006a), the dietary evolution of herbivores (Domingo *et al*. 2009, 2012) or by changes in the mineral composition of the sediments present in the Somosaguas fossil site (Carrasco *et al*. 2008).

The aim of this research is to detect changes in the prey's community structure through time and to relate these changes to several major climatic fluctuations that took place during the middle Aragonian (middle Miocene). Thus, in order to evaluate the climatic evolution of the Madrid Basin before and after the middle Miocene Global Cooling Event, we applied two classic palaeo-synecological methodologies traditionally used for this purpose; cenograms (developed by Valverde (1964) and palaeoenvironmentally applied by Legendre in 1986 and 1989) and body size diversity (developed by Fleming (1973) and applied to the fossil record by Andrews *et al*. 1979) to the mammalian fauna from six different localities in the Madrid Basin. These localities are placed on the Lower or Middle Unit (Calvo 2000, Montes *et al*. 2006, Domingo *et al*. 2009), covering local biozones Dc to G (15.5 to 13.5 Ma) according to the micromammal biozonation established by Daams *et al*. (1999) for the Calatayud-Daroca Basin and recognized in the Madrid Basin by Peláez-Campomanes *et al*. (2003). The analysed interval (2 million years) represents a good example to assess this environmental change, because it covers the end of the Miocene Climatic Optimum, together with the end of the Global Cooling Event (Zachos *et al.* 2001).

Additionally, in order to generate a comparative framework to assign a specific biome to each fossil assemblage, we described the body size community structures for mammalian prey of 100 modern localities. Finally, since the geological and environmental histories of the continents determine the faunal composition of the different regions (Pickford & Morales 1994, Moreno Bofarull *et al.* 2008) and are relevant factors for the mammalian community structure (Croft 2001, Nieto & Rodríguez 2003, García Yelo *et al.* 2009), the influence of biogeography on the relationships was also analysed.

Material and Methods

Extant and fossil faunas

In order to establish our comparative framework and to test the relationship between body size community structure and climate, we used the climatic data (type of biome) and the mammalian prey faunal data from 100 extant localities (fig. 3.1, appendix 1) uniformly distributed around the world (excluding Australia). Here we followed the biome characterization from Walter (1970), and modified by Hernández Fernández (2001), which represents the 10 climate types present in the Earth today (I: evergreen tropical rainforest; II: tropical deciduous woodland; II/III: savannah; III: tropical desert; IV: sclerophyllous woodland; V: temperate evergreen forest; VI: nemoral broadleaf-deciduous forest; VII: steppe; VIII: taiga; IX: tundra). Marine and flying mammals, as well as the species introduced by anthropic action, were excluded from our analysis. Nevertheless, those species that were extinct during historic times were incorporated in the database. Taxonomy was standardized to Wilson and Reeder (1993). The body size data for modern species were obtained from Smith *et al.* (2003). For the few species with no body size information, the mean of the genera was calculated (Rodríguez 1999, Croft 2001, Hernández Fernández *et al.* 2006a). Here we use the concept prey mammals as any terrestrial species, excluding the Australian ones, not belonging to the order Carnivora (Orders Didelphimorphia, Paucituberculata, Microbiotheria, Tubulidentata, Macroscelidea, Hyracoidea, Proboscidea, Xenarthra, Scandentia, Dermoptera, Primates, Rodentia, Lagomorpha, Insectivora, Pholidota, Perissodactyla, and Artiodactyla).

In order to evaluate the climatic evolution of the Madrid Basin before and after the middle Miocene Global Cooling Event, we analysed the body size community structure of prey from six middle Miocene fossil sites from the Madrid Basin (fig.

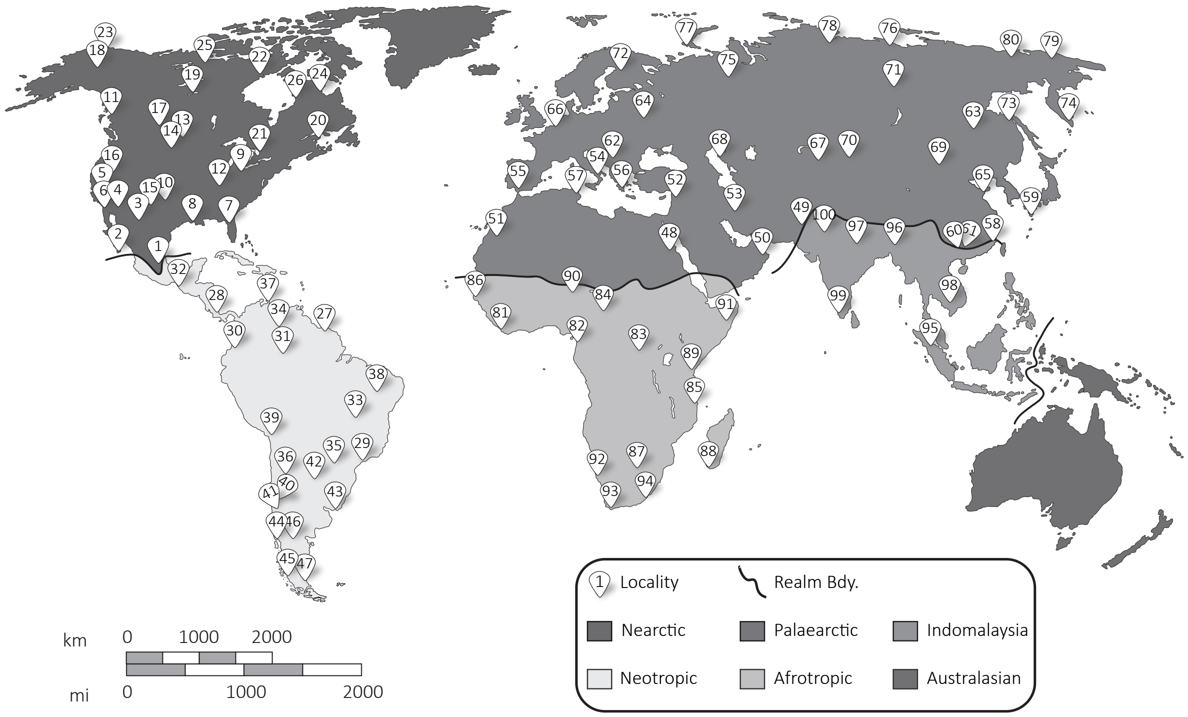


Figure 3.1. *Distribution of the 100 modern communities studied in this work. Numbering as in appendix 1. The different grey shades indicate the different biogeographical realms (light black: Palearctic; dark grey: Nearctic; grey: Afrotropic; silver: Indomalaysia; light grey: Neotropic).*

3.2). These localities are: Estación Imperial; Paseo de las Acacias; Arroyo del Olivar-Puente de Vallecas; Somosaguas; Paracuellos 5 and Paracuellos 3. The faunal list of the six localities, together with the body size for fossil species were obtained from Peláez-Campomanes *et al.* (2003), Hernández Fernández *et al.* (2006b), Perales *et al.* (2009) and Hernández-Ballarín *et al.* (2011), and are detailed in supplementary data 3.1. These fossil sites are among the most completely sampled of the Madrid Basin for this period, with a total of 54 species represented and more than 18000 pieces recuperated in successive field works (supplementary data 3.1).

Body size Community Structure and Discriminant Analysis

We used two palaeo-synecological methodologies, cenograms (Legendre 1986, 1989) and body size spectra (Andrews *et al.* 1979), to describe the community structure of the mammals present in each locality. Originally, these methodologies were used to visually compare fossil community structure patterns with those from recent mammalian communities and then try to assign a particular habitat to the fossil community.

In body size spectra, every prey mammal from a particular community is

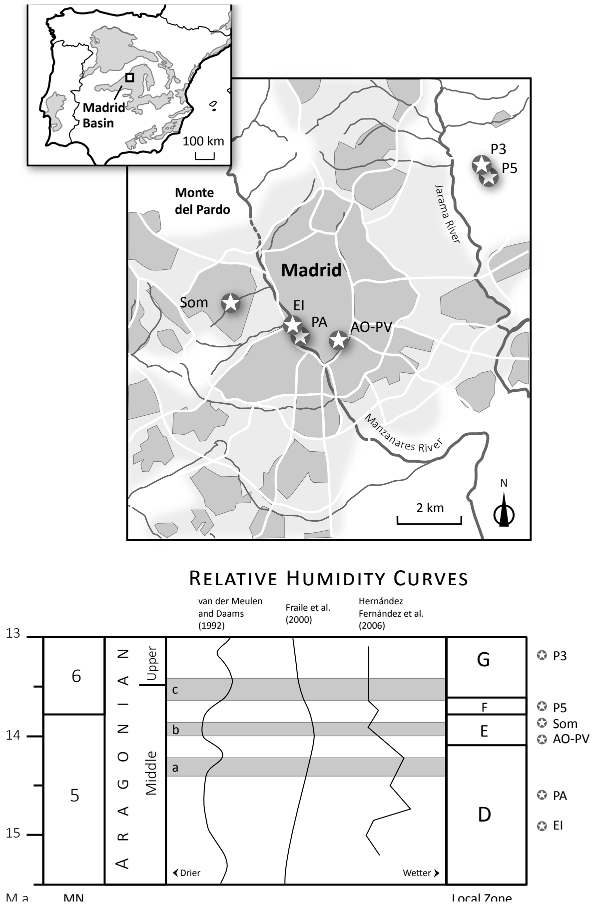


Figure 3.2. *Temporal and geographical situation of the six fossil sites used in this analysis. The relative humidity curves of van der Meulen and Daams (1992), Fraile et al. (2000) and Hernández Fernández et al. (2006) are also included to compare with our results. The grey lines indicate the pulses of changes in the aridity conditions. Abbreviations are used as follows: Estación Imperial (EI); Paseo de las Acacias (PA); Arroyo del Olivar – Puente de Vallecas (AO-PV); Somosaguas (Som); Paracuellos 5 (P5) and Paracuellos 3 (P3).*

assigned to one of the body size categories defined in table 3.1 (Andrews *et al.* 1979, Hernández Fernández *et al.* 2006a). Once each species of the prey community was classified in one of the body size categories and the final sum for each category converted to a percentage, the body size spectrum of the community was obtained. For Legendre's methodology, rank ordered taxa ***vs***. body size graphs were plotted. Species were then separated according to body size in four categories, small prey (< 500 g), medium prey (500 g - 8 Kg), large prey (8 - 1000 Kg) and mega-prey (≥ 1000 Kg) (Legendre 1986, 1989, Rodríguez 1999, Hernández Fernández *et al.* 2006a). Rodriguez's (1999) stated that these body-size thresholds, defined by previous authors (Legendre 1989, Gingerich 1989), respond to trophic and physiological constraints. As mega-prey species are restricted to a few tropical localities, they were excluded from the analysis in order to make the results more comparable among the different communities. Finally, twelve cenogram variables (fig. 3.3, table 3.2) were defined to describe the mammalian body size structure of the communities. Both Rodríguez (1999) and Hernández Fernández *et al.* (2006a) selected these variables because of their ecological significance. Although the limits between categories are fixed, the number of species present in those categories can vary as a consequence of the predator pressure (Valverde 1967). Thus, while the different mean weight or body mass (Wx) reveals the more suitable size to avoid predator pressure in each category, the magnitude of the different gaps (G, mG and MG) and its position on the cenogram

(WG, WmG and WMG) depict exactly the opposite. Finally the slopes in the cenogram were defined in order to state the species-richness in each category (Gingerich 1989).

BODY SIZE SPECTRA CATGORIES	
Category	Weight range (g)
A	0 - 100
B	100.1 - 1000
C	1000.1- 10000
D	10000.1 - 45000
E	45000.1 - 90000
F	90000.1 - 180000
G	180000.1 - 360000
H	> 360000

Table 3.1. *Body size categories defined to determine the body size spectra of the mammalian communities used in our study (Andrews et al. 1979, Hernández Fernández et al. 2006).*

Taphonomic and sampling biases might have affected mammalian diversity and structure of the fossil communities, making a rarefaction analysis necessary. Nevertheless, as previous studies have revealed, a high number of species have to be lost to significantly affect the structure of a community (Gómez Cano *et al.* 2006). Due to the high sample size of the fossil sites used in this study, the possibility of this kind of biases may be discarded.

Once the community structure and biome of modern faunas were defined in each locality, we tried to establish a statistical relation between the type of biome and a specific community structure pattern. Following Hernández Fernández *et al.* (2006a) we performed a multivariate discriminant analysis of the dataset containing modern faunal information in order to assess the statistical capability of both methodologies to distinguish between biomes. In a second analysis the different biogeographic histories of the continents were taken into account; thus, the test was repeated independently with localities grouped by their respective biogeographic realms. Conceptually, this forced us to remove from the study those localities that belong to biomes represented by only one community in a biogeographic realm. Consequently, only tropical biomes are represented in the tropical realms of the Old World, and the Indomalaysian region only included evergreen tropical rainforest and tropical deciduous woodland biomes. Additionally, due to a likely Palaeotropical

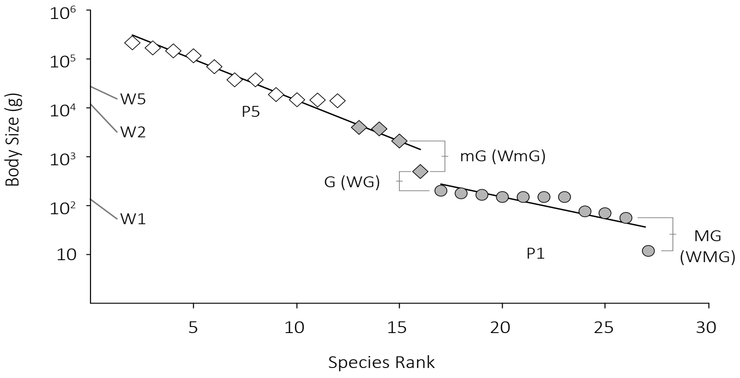


Figure 3.3. *Cenogram associated with the mammal community of Patna (India). Grey circles, small prey; grey diamonds, middle-size prey; white diamonds, large prey. Variables of the cenogram as in table 3.2.*

CENOGRAM VARIABLES	
Variables	Description
W1	Mean weight or body mass of all small prey (< 500 g) (in logarithmic units)
W2	Mean weight or body mass of all medium prey (500 g – 8 Kg) (in logarithmic units)
W5	Mean weight or body mass of all medium-large prey (500 g – 1000 Kg) (in logarithmic units)
P1	Slope of the line segment determined by small prey (< 500 g)
P5	Slope of the line segment determined by medium-large prey (500 g – 1000 Kg)
P5-P1	Difference in slope between the line segments determined by medium-large and small prey
G	Magnitude of the gap between small and medium-large prey (in logarithmic units)
mG	Magnitude of the major gap between two consecutive species of medium-large prey (in logarithmic units)
MG	Magnitude of the major gap between two consecutive species of all prey (in logarithmic units)
WG	Mean weight or body mass of the two species that define G (in logarithmic units)
WmG	Mean weight or body mass of the two species that define mG (in logarithmic units)
WMG	Mean weight or body mass of the two species that define MG (in logarithmic units)

Table 3.2. *Cenogram variables defined to describe the mammal community structure based on the cenogram methodology (Valverde 1964, 1967, Hernández Fernández et al. 2006).*

origin of the Miocene mammals from the Iberian Peninsula (Pickford & Morales 1994) and the climatic similarities between the modern tropical realms and the Iberian Peninsula during the Miocene (Hernández Fernández *et al.* 2006a), we carried out a new analysis where the localities within the Afrotropical and Indomalaysian realms were grouped together. Thus, the biomic inference for the fossil sites was based on the Afrotropical, Indomalaysian and Palaeotropical discriminant models.

Results

Discriminant analyses applied to body size spectra and cenogram variables from the modern fauna have shown a low biome discriminant capability of both methodologies at the global scale (47% and 55.7% of correctly classified localities respectively). However, our results were significantly improved when the analyses were repeated separating communities by biogeographic realms (table 3.3), indicating a noteworthy influence of the evolutionary history on prey community structure based on their body size distributions.

In order to examine which body size variables made the strongest contribution to discriminate biomes in every analysis, the principal components that discriminate biomes in our study have been studied (supplementary data 3.2). While for cenogram

		N INCLUDED BIOMES	CORRECTLY CLASSIFIED COMMUNITIES	
			BSS	CENOGRAMS
	GLOBAL	100* (I-IX)	47.0%	55.7%
BIOGEOGRAPHIC REALM	NEARCTIC	26 (II/III-IX)	65.4%	96.2%
	NEOTROPIC	19* (I,II,II/III,V,VII)**	73.7%	100.0%
	PALEARCTIC	33* (III-IX)	72.7%	84.4%
	AFROTROPIC	12 (I-III)	91.7%	100.0%
	INDOMALAYSIA	5 (I-II)	100.0%	60.0%
	PALEOTROPIC	18 (I-III)	77.80%	100.0%

Table 3.3. *Results of the discriminant analyses for the extant communities at global level and by biogeographic realms (biome clasification as in the text). *The N (numbers of localities) noted with an asterisk reflects those cases where the localities included in the analysis are not the same for both methodologies (given number refers to the BBS method). The number of included localities for cenogram method is: 97 (for global analysis), 15 (for Neotropic) and 32 (for Palaearctic) **The double asterisk indicates that the number of biomes included in the Neotropics is also different in both methods, being the given biomes those for the BBS method, while for cenogram method are I, II, II/III and V.*

global analysis are the slope variables (P5, P5-P1, G, W1 and WG) the principal ones that contribute to discriminate biomes, for the biogeographic realms analyses different variables contribute to separate biomes in every region. While for the Indomalaysian realm the mean weight variables (W1, W2 and W5) are the ones that discriminate biomes, for the Afrotropic and the Palaeotropic most of the cenogram variables seem to help to discriminate biomes. In the body size spectra case, body size categories A and E are the main contributors to the global discrimination of biomes. Nevertheless, when the discriminant analyses are repeated by biogeographic realms, different categories separate biomes in each biogeographic region, with all body size categories being represented (supplementary data 3.2).

Once the discriminant models for the Afrotropical, Indomalaysian and Palaeotropical realms were performed, the biomic inference for the six fossil sites were obtained (table 3.4). Given a particular biogeographic region (e.g., Afrotropic), the inferred biome for the same fossil locality (e.g., Estación Imperial) is different using each methodology (tropical deciduous woodland and tropical desert). All predicted biomes, excluding the evergreen tropical rainforest detected by the Indomalaysian realm, are arid and warm.

		EI	PA	AO-PV	Som	P5	P3
BODY SIZE SPECTRA	AFROTROPIC	II	II	II	II	II	II
	INDOMALAYSIA	I	I	I	I	I	II
	PALAEOTROPIC	III	III	II	II/III	II/III	II
CENOGRAM	AFROTROPIC	III	III	II/III	III	II/III	II/III
	INDOMALAYSIA	II	II	I	II	II	I
	PALAEOTROPIC	III	II	II	III	III	II

Table 3.4. *Inferred biomes for the six fossil sites included in the analysis. The grey colours represent different trends in the hydric gradient; relatively more humid climates are marked with grey and relatively more arid biomes with white. Abbreviations are used as follows: Estación Imperial (EI); Paseo de las Acacias (PA); Arroyo del Olivar – Puente de Vallecas (AO-PV); Somosaguas (Som); Paracuellos 5 (P5) and Paracuellos 3 (P3).*

These results are complex and make the use of both methodologies to infer biomes complicated. Nevertheless, a common pattern can be asserted. Changes in the aridity and forest density through time can be detected by cenograms (for all realms analysed) and the body size spectra (for the Palaeotropical realm). It is worth mentioning that most of these changes are detected synchronously by both methods in most of the cases (table 3.4). The studied period started with an arid/semiarid and scarcely forested environment (II or III biomes were obtained for Estación Imperial and Paseo de las Acacias) that was followed by a climatic change to relative more wooded-humid conditions between biozones D and E (I, II, II/III biomes for Arroyo del Olivar-Puente de Vallecas). After a short lapse of time (still inside biozone E), arid and less forested conditions returned (II, II/III or III for Somosaguas and Paracuellos 5). Finally, a new environmental change to more forested and humid conditions (I, II, II/III biomes for Paracuellos 3) took place between biozones F and G.

Nevertheless, it is also worth mentioninig that the results given by the body size spectra for the Indomalaysian realm show an homogeneous climate during most of the sequence excepting at the end, where a climatic change between humid to arid conditions (from biome I to II) was produced, showing an inversion of the pattern (table 3.4). Finally, regardless of the high inference potential of the body size spectra for the modern localities of the Afrotropical region, this method does not detect any environmental change for the whole sequence of the fossil sites under study.

Discussion

Our results show changes in climate during the middle Miocene in the Madrid Basin, with a fluctuation between arid and relatively more humid conditions. All the

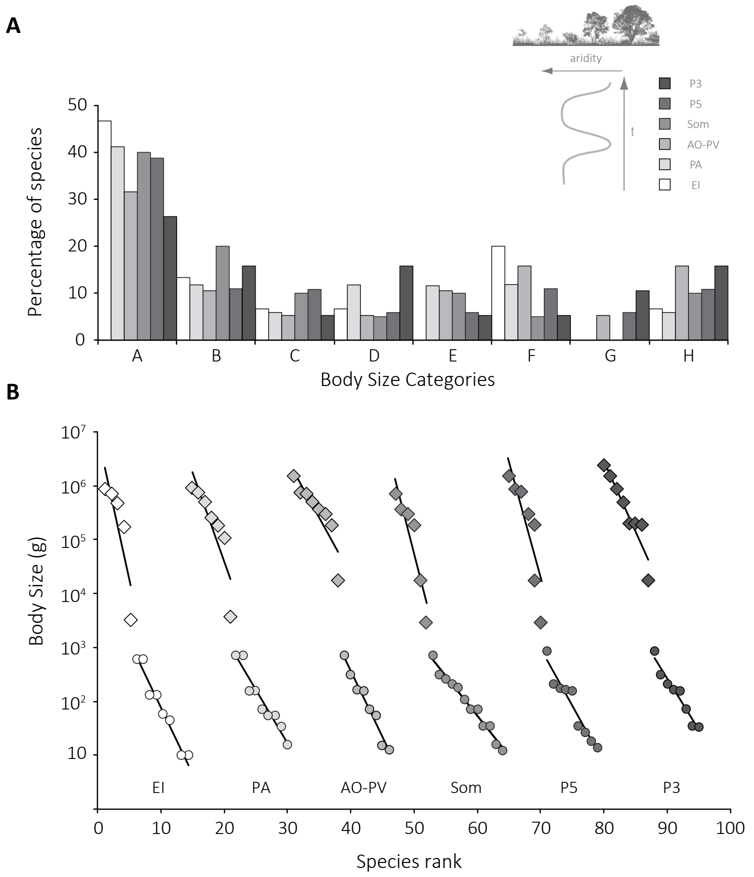


Figure 3.4. *Resume figure with a compendium of the six body size spectra (A) and the cenograms (B) obtained for the Aragonian palaeocommunities. A schematic aridity curve is provided for the analysis interval. Abbreviations are used as follows: Estación Imperial (EI); Paseo de las Acacias (PA); Arroyo del Olivar – Puente de Vallecas (AO-PV); Somosaguas (Som); Paracuellos 5 (P5) and Paracuellos 3 (P3).*

climates inferred for the different fossil sites in this research are tropical, and most of them show aridity at some level. Previous studies also found a tropical warm and arid climate for the Iberian Peninsula during this time span. Amezua *et al.* (2000) used several palaeo-synecological methodologies (ecological diversity spectra, cenograms, diversity indexes, quantitative species composition and presence/absence of environmental indicative species) to analyse the environmental evolution of the Madrid Basin over the middle Aragonian. They found very homogeneous conditions for the Madrid Basin through the middle Miocene, with warm and arid environments with slight variations in the humidity. Hernández Fernández *et al.* (2006a) also used ecological diversity and cenograms to recognise aridity peaks, by means of biome characterization, through the middle Aragonian of Spain. All fossil sites were classified as tropical deciduous forest (II), savannah (II/III) or tropical desert (III) (excluding three of them classified as temperate evergreen forest by the trophic diversity model), which are warm and relatively arid biomes. Costeur and Legendre (2008) analysed the mammalian body-weight structure of 17 fossil communities from middle Miocene (17-14 M.a.) from Spain and Germany, finding a southwest-northeast latitudinal environmental gradient, from a warm, arid and open environment in Spain to a warm, closed and humid environment in Germany.

In most of the discriminant models a common pattern can be detected. At the beginning (coincidently with the Miocene Climatic Optimum) and the middle of the sequence (after the Global Cooling Event), two lapses of time corresponding to local zones Dc and E-F (including Estación Imperial, Paseo de las Acacias, Somosaguas and Paracuellos 5 fossil sites), the prey community structures of the fauna present in the Madrid Basin reflect more open and arid conditions (desert, tropical deciduous woodland or savannah) than the rest of the sequence in the different discriminant models. The rest of the sequence (Arroyo del Olivar-Puente de Vallecas and Paracuellos 3 fossil site communities) represents more humid and closed environments (evergreen tropical rainforest, tropical deciduous woodland or savannah). Although the same biome classification was estimated for some sites of both environment types, arid and relatively humid localities, such overlap is rarely obtained within the same discriminant model. Our results suggest that three environmental fluctuations took place during this period. The first and third climatic changes (between Paseo de las Acacias and Arroyo del Olivar-Puente de Vallecas, and between Paracuellos 5 and Paracuellos 3) were toward relatively more humid and forested conditions. The second one (between Arroyo del Olivar-Puente de Vallecas and Somosaguas) coincided with the middle Miocene Global Cooling Event and reflects more arid conditions. The relative humidity curves given by Meulen and Daams (1992) and Hernández Fernández *et al.* (2006b), based in changes in the structure of rodent faunas, depict aridity peaks that match in time with the climatic change towards more open and arid environments detected in the present study (fig. 3.2). Fraile *et al.* (2000) also detected these changes in mammal faunas from the Madrid Basin although they noticed small differences on the time limits between arid and humid environments (fig. 3.2). Finally, isotopic analysis of tooth enamel of middle Miocene ungulates from the Madrid Basin also shows similar results, with fluctuations between arid and relatively humid periods (Domingo *et al.* 2012).

When the six body size spectra and cenograms from the fossil communities are represented together (fig. 3.4), further interpretations can be made. James (1970) found that birds in cold and dry environments were smaller than their relatives in warm and humid ones, so the relative large ***vs.*** small birds ratio should grow from dry to humid environments. If we extrapolate this concept to mammalian communities, the proportion of small species should decrease from dry environments to humid ones, whereas large species would become more frequent as the aridity of the environment decreases. Analysing the body size spectrum of the different extinct communities (fig. 3.4A), different ratios of large *vs*. small mammals can be noticed. In dryer localities (Estación Imperial, Paseo de las Acacias, Somosaguas and Paracuellos 5), small mammals (characterized by body size category A) are over represented (above the 40%; μ=42.25%), and the large *vs.* small mammals (categories G and H; cat[G+H]/catA ratio) ratio is small (μ=0.24). On the other hand, in relatively more humid localities (Arroyo del Olivar-Puente de Vallecas and Paracuellos 3), small mammals are drastically reduced (in both cases under the 32%; μ=28.95%) and the large ***vs.*** small mammals ratio is higher (μ=0.83). These differences in the body size diversity structure between arid and relatively humid fossil communities are statistically significant (small mammals: T=-4.816, p=0.009; large *vs.* small mammals ratio: T=4.122, p=0.015). Nevertheless, these differences have not been found in the modern fauna (small mammals: μ_{humid}=48.94%,μ_{arid}=43.92%, T=1.783, p=0.078; large *vs.* small mammals ratio: μ_{humid}=0.08, μ_{arid}=0.12, T=-1.538, p =0.128), maybe as a consequence of the interaction of some other climatic factors, such as temperature, over the body size of mammals (Bergmann rule).

This pattern is also reflected for macromammals in the cenogram structure of the different fossil communities (fig. 3.4B), where the slope of the line that defines medium-large prey (P5) is statistically different between arid and relatively humid fossil sites (T=-3.078, p=0.037), being more pronounced in arid localities (μ=-0.88) than in the relatively humid ones (μ=-0.47). Furthermore, these differences are also detected in the modern fauna (μ_{humid}=-1.02; μ_{arid}=-0.695; T=2.099, p=0.039). Interestingly, the cenograms for these fossil sites contradict one of the most accepted rules for aridity and cenogram structure. As Legendre defined (1986, 1989), the magnitude of the gap between small and medium-large prey is related to the aridity of the environment; the more arid the climate is, the larger the gap. But in our results statistically larger gaps are present in the humid localities (T=-9.729, p=0.001; μ_{humid}=2.70; μ_{arid}=1.28). Again, these differences are also detected in the modern fauna (μ_{humid}=1.32; μ_{arid}=0.93; T=-2.092, p=0.040). In the fossil sites, this is a consequence of the absence in Arroyo del Olivar-Puente de Vallecas and Paracuellos 3 of the species *Cainotherium miocaenicum* or a member of the genus *Amphechinus*, the latter showing a clear preference for arid environments (Furió *et al.* 2011). This fact could be a consequence of taphonomic bias against the preservation of small mammals in closed environments (Cantalapiedra *et al*. 2012), but since this difference is also detected in the modern fauna, we suggest that this pattern could be a consequence of the higher hydric constrictions of large prey mammals. Water is an environmental conditioning factor that forces large animals to inhabit preferentially more closed and humid environments (Robertshaw & Taylor 1969, McNab 2002) and consequently, smaller species would find benefits in get adapted to arid environments in order to avoid competition.

Also the species composition of the fossil sites corroborates our results. An important proportion of the species of our fossil communities are typically arid-adapted taxa, as inhabitants of arid localities. However, the presence of a few taxa allows us to assess further details of the environment (more arid and open, or more humid and close). For example, arid conditions are reflected in the presence of *Hispanotherium matritense* or *Anchitherium cursor*, two perissodactyls with hypsodont dentition and relatively gracile limbs that are adapted to open and arid conditions (Cerdeño & Nieto 1995, Soria *et al.* 2000, Salesa *et al.* 2001, Hernández Fernández *et al.* 2003), or several members of the order Rodentia, such as *Armantomys*, *Microdyromys*, *Democricetodon* or *Cricetodon* (Weerd & Daams 1978, Meulen & de Bruijn 1982, Daams & Meulen 1984, Mein 1983, Sesé *et al.* 1985). This supports the idea of a more arid an open environment for Estación Imperial, Paseo de las Acacias, Somosaguas and Paracuellos 5 fossil sites. On the contrary, all these taxa are absent in Arroyo del Olivar-Puente de Vallecas and Paracuellos 3, whereas other forest-adapted dwellers are found, pointing to a more closed and less arid environment. Some examples of such forest-adapted faunas are *Chalicotherium grande*, a perissodactyl with longer forelimbs and a brachiodont dentition (Sánchez 2000); cervids such as *Euprox furcatus*, a browser with preferences for arboreal vegetation (Soria *et al.* 2000), or the rhinoceros *Lartetotherium sansaniense* with shorter and slightly more robust limbs than *Hispanotherium* (Sánchez-Chillón & Cerdeño 2000).

Additionally, the presence of thermophile species, such as *Lagopsis penai, Lagopsis verus*, *Microdyromys koenigswaldi*, *Microdyromys monspeliensis* (López Martínez 1977, Meulen & de Bruijn 1982, Daams & Meulen 1984, Mein, 1983, Sesé *et al.*, 1985, Luis & Hernando 2000) in all the fossil localities confirms the warm conditions of the Madrid Basin during the sequence.

Conclusions

While at the global scale body size spectra and cenogram methodologies seem to have low capability to discriminate biomes from the data in modern localities, when the biogeographic histories of modern faunas are considered, body size community structure of prey mammals emerges as a good proxy for inferring biomes. Nevertheless, when the method is applied to the fossil record, the biome inferences may appear inaccurate, although fluctuations in climate and environments are precisely recovered.

Compared with the extant mammals from the Palaeotropics, the body size community structures of the Aragonian mammals present in the Madrid Basin allowed us to infer a predominance of semiarid environments between 15.5 and 13.5 Ma. Additionally, the methodologies used here allowed us to clearly distinguish several pulses of distinctive aridity throughout the whole sequence. A phase of arid climate and open environments was detected at the beginning of the sequence (Estación Imperial and Paseo de las Acacias fossil sites), which was followed by an environmental change towards a more humid and forested phase (Arroyo del Olivar-

Puente de Vallecas). Arid conditions and grass-dominated habitats returned to central Iberia associated to the Global Cooling Event of the middle Miocene (coinciding with Somosaguas fossil site age). At the end of the sequence (Paracuellos 3 fossil site) the landscape returned to a more covered and humid scenario.

When the body size community structure of the fossil faunas was deeply analysed, a positive influence of the aridity over the relative percentages of small prey was recovered. Nevertheless, this influence is masked by other climatic factors (*e.g.* temperature) in the actual faunas. Nonetheless, cenogram methodology also detects this influence, not only in fossil sites, but also in the extant mammalian communities. The slope of the line that defines medium to large prey (P5) is more marked in arid environments than in relatively more humid ones. The magnitude of the gap between small and medium-large (G) prey also shows this influence, having bigger gaps in humid localities. This contradicts Legendre's more accepted rules over cenograms, which stated that the more arid the environment is, the larger the gap between small and medium-large prey. Nevertheless, our methodology uses a macro-scale approach to analyse climatic evolution, and some differences are expected if a smaller geographical scale is taken into account.

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Supplementary data

Supplementary data 3.1. *Faunal lists for the six fossil site included in the analysis.*

DEPOSITIONAL UNIT	MIDDLE UNIT				LOWER UNIT		BODY WEIGHT (LN)
LOCAL ZONE	D		E		F	G	
FOSSIL SITE	EI	PA	AOPV	S	P5	P3	
Euprox furcatus						x	10.62
Heteroprox larteti						x	10.60
H. moralesi			x	x	x		10.96
Procervulus dichotomus		x					10.82
Micromeryx flourensianus			x		x	x	8.48
M. sp. cf. M. flourensianus				x			8.48
Palaeomeryx magnus			x		x	x	12.38
Triceromeryx pachecoi	x	x					11.92
Dorcatherium crassum		x					10.09
Tethytragus sp.	x	x	x	x	x		10.53
T. langai						x	10.53
Conohyus simorrensis			x	x			11.70
Bunolistriodon lockharti	x	x	x				11.73
Listriodon splendens					x	x	11.87
Alicornops simorrensis						x	14.64
Cainotherium miocaenicum	x	x					7.15
Hispanotherium matritensis	x	x					14.09
Hoploaceratherium tetradactylum			x		x		14.11
Lartetotherium sansaniense						x	13.85
Prosantorhinus douvillei				x			14.26
Rhinocerotidae indet			x				14.07
Anchitherium sp.						x	11.41
A. alberdidae		x					11.35
A. cursor			x	x			11.12
A. matritensis	x		x				11.42
A. procerum					x		11.79
Chalicotherium grande						x	12.76
Gomphotherium angustidens			x	x	x	x	14.64
Amphechinus sp.				x			6.92
A. cf. intermedius					x		6.92
Crocidosoricinae indet					x		2.30
Soricidae indet	x		x	x			2.20
Galerix sp.			x		x	x	4.45
G. exilis				x			4.04
Lagopsis verus					x	x	5.86
L. penai	x	x	x	x			5.70
Prolagus sp.				x	x		4.50
Democricetodon sp.	x	x		x			3.71
D. larteti			x	x		x	3.71
Megacricetodon collongensis	x	x	x				2.40

Supplementary data 3.1. *Continued.*

DEPOSITIONAL UNIT	MIDDLE UNIT				LOWER UNIT		BODY WEIGHT (LN)
LOCAL ZONE	D		E		F	G	
FOSSIL SITE	EI	PA	AOPV	S	P5	P3	
Megacricetodon crusafonti						x	3.04
Megacricetodon gersii					x		2.83
Megacricetodon rafaeli					x		2.48
Megacricetodon sp. cf. M. collongensis				x			2.40
Cricetodon soriae				x			4.86
Microdyromys monspeliensis				x			3.09
Microdyromys koenigswaldi		x		x	x	x	3.09
Microdyromys sp.	x						2.20
Simplomys simplicidens	x	x	x				3.48
Armantomys aragonensis	x	x	x				4.39
Armantomys jasperi		x					3.50
Armantomys tricristatus				x	x	x	4.65
Heteroxerus grivensis			x	x		x	4.98
Heteroxerus rubricati	x	x			x	x	4.39
Atlantoxerus blacki	x	x					5.72

Supplementary data 3.2a. *Eigenvalues and correlation tables between the body size spectra categories and the discriminant functions obtained for global and biogeographic realms analyses*

Global Analysis

Eigenvalues				
Function	Eigen-value	% of Variance	Cumulative %	Canonical Correlation
1	2.361	66.2	66.2	0.838
2	0.606	17	83.2	0.614
3	0.303	8.5	91.7	0.483
4	0.181	5.1	96.7	0.392
5	0.076	2.1	98.9	0.266
6	0.038	1.1	99.9	0.191
7	0.002	0.1	100	0.05

	Standarized Canonical Coefficients						
	Function						
	1	2	3	4	5	6	7
CAT. A	1.685	0.581	1.883	0.762	0.627	1.663	2.578
CAT. B	0.680	0.631	0.928	0.807	0.191	1.925	1.750
CAT. C	0.691	-0.076	1.105	0.611	1.140	1.341	2.008
CAT. D	0.151	0.042	1.341	0.305	-0.190	0.966	1.753
CAT. E	1.105	-0.375	0.467	-0.001	-0.024	1.290	1.133
CAT. F	0.552	0.445	0.095	-0.593	0.489	0.605	1.099
CAT. G	0.671	-0.096	-0.199	0.753	-0.053	0.283	1.111

Biogeographic Analyses

Afrotropical Realm

Eigenvalues				
Function	Eigen-value	% of Variance	Cumulative %	Canonical Correlation
1	10.478	73.3	73.3	0.955
2	3.325	23.3	96.6	0.877
3	0.492	3.4	100	0.574

Standarized Canonical Coefficients			
	Function		
	1	2	3
CAT. A	2.362	1.176	0.103
CAT. B	4.008	3.579	1.036
CAT. C	1.838	0.724	0.961
CAT. D	4.442	2.681	0.921
CAT. E	0.596	-0.090	0.835
CAT. F	-0.369	1.558	0.275

Indomalaysian Realm

Eigenvalues				
Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	442.601	100	100	0.999

Standarized Canonical Coefficients	
	Function
	1
CAT. A	23.081
CAT. B	18.246
CAT. C	-9.156

Paleotropic realm

Eigenvalues				
Function	Eigen-value	% of Variance	Cumulative %	Canonical Correlation
1	1.821	58.6	58.6	0.803
2	0.856	27.6	86.2	0.679
3	0.429	13.8	100	0.548

Standarized Canonical Coefficients			
	Function		
	1	2	3
CAT. A	1,259	2,377	0,629
CAT. B	0,082	2,434	-0,132
CAT. C	0,208	2,479	0,978
CAT. D	0,611	2,195	0,197
CAT. E	-0,580	1,245	0,663
CAT. F	0,337	0,449	1,557
CAT. G	-0,792	-0,099	-0,689

Supplementary data 3.2b. *Eigenvalues and correlation tables between the cenogram variables and the discriminant functions obtained for global and biogeographic realms analyses.*

Global Analysis

Eigenvalues				
Function	Eigen-value	% of Variance	Cumulative %	Canonical Correlation
1	4.495	63.1	63.1	0.904
2	1.33	18.7	81.7	0.756
3	0.619	8.7	90.4	0.618
4	0.325	4.6	95	0.495
5	0.203	2.8	97.8	0.41
6	0.079	1.1	98.9	0.27
7	0.037	0.5	99.4	0.188
8	0.03	0.4	99.9	0.172
9	0.01	0.1	100	0.099

	Standarized Canonical Coefficients								
	Function								
	1	2	3	4	5	6	7	8	9
W1	0.511	-0.449	-0.227	0.523	0.559	0.253	0.223	0.100	-0.256
W2	-0.018	-0.972	0.608	-0.196	-1.178	-0.031	0.486	0.051	-0.662
W5	-0.015	0.296	0.014	0.271	0.303	0.250	0.447	0.188	0.137
P1	0.015	0.053	0.173	0.033	0.075	-0.372	-0.038	0.447	-0.074
P5	1.455	1.017	0.011	0.069	-0.444	0.206	1.083	0.109	0.699
P5-P1	-1.099	-0.678	-0.219	-0.222	0.325	0.077	-0.308	0.422	-0.162
G	-0.966	0.112	-0.551	-0.422	1.232	-0.170	0.262	0.727	0.312
mG	-0.677	0.265	0.741	-0.233	0.291	-0.957	1.357	0.690	-0.287
MG	0.835	0.133	-0.262	0.950	-1.150	1.311	-0.554	-0.581	0.680
WG	0.241	0.991	0.060	-0.493	0.499	0.338	-0.078	-0.435	-0.129
WmG	0.298	-0.450	0.779	-0.073	0.419	0.129	-0.130	-0.069	0.399
WMG	-0.146	0.367	-0.190	0.242	-0.166	0.552	-0.285	0.690	-0.442

Biogeographic Analyses

Afrotropical Realm

Eigenvalues				
Function	Eigen-value	% of Variance	Cumulative %	Canonical Correlation
1	204.547	85.5	85.5	0.998
2	27.908	11.7	97.2	0.983
3	6.716	2.8	100	0.933

Standarized Canonical Coefficients			
	Function		
	1	2	3
W1	1.530	-1.417	0.031
W2	21.974	1.133	-2.185
W5	-4.590	-4.904	0.304
P1	-14.198	-12.018	3.507
P5	1.222	16.715	-0.839
G	7.554	5.647	1.239
mG	-0.874	6.409	4.639
MG	4.357	-6.061	-4.735

Indomalaysian Realm

Eigenvalues				
Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	0.573	100	100	0,604

Standarized Canonical Coefficients	
	Function
	1
W1	0.415
W2	0.678
W5	-0,764

Supplementary data 3.2b. *Continued.*

Biogeographic Analyses

Paleotropic realm

Eigenvalues				
Function	Eigen-value	% of Variance	Cumulative %	Canonical Correlation
1	13,813	68	68	0,966
2	4,24	20,9	88,9	0,9
3	2,263	11,1	100	0,833

Standarized Canonical Coefficients			
	Function		
	1	2	3
W1	3.739	1.888	1.593
W2	-1.168	-0.085	1.490
W5	2.736	3.552	0.888
P1	-1.518	3.482	-1.557
P5	1.595	-6.404	-0.453
G	1.574	0.935	1.841
mG	4.510	-0.172	1.040
MG	-5.352	0.182	-2.508
WG	2.551	3.769	0.509
WmG	2.910	1.341	0.619
WMG	-1.062	0.658	-0.310

4. HISTORICAL AND CLIMATIC INFLUENCE ON THE FUNCTIONAL STRUCTURE OF MAMMALIAN CARNIVORE COMMUNITIES.

Abstract

The ecology of carnivore mammals has traditionally been considered to rely on prey availability and behaviour. The surrounding environment, however, has a noteworthy influence thereupon. The climatic influence on the community structure of mammalian faunas has previously been established, through consideration of the community as a whole or of the herbivore fauna. The main objective of the present research involved determining the relationship between the environment and the functional structure of carnivore mammals (Carnivora, Mammalia). By means of cluster analysis, we defined eleven functional groups based on body size, hunting locomotor behaviour and feeding habits, of all terrestrial species belonging to the order Carnivora (250 species). Subsequently, the community structure of 100 modern localities, pertaining to the ten different biomes found on Earth today, was described by means of its carnivore functional spectra. We defined the bioclimatic signal of each functional group by means of one-way ANOVA analyses. Finally, discriminant analyses were performed in order to establish a relationship between the type of biome and the carnivore functional spectrum of these localities. We first considered all communities together and then repeated the analyses, separating them into biogeographic realms. The clustering process shows the high level of influence of the feeding and locomotor behaviour patterns of mammal predators associated with the energy constraints imposed by both ecological factors in the niche development of the species. Whereas 56% of cases were correctly classified on considering all communities together, the analyses of the biogeographical realms provided percentages of correctly classified cases of over 80% in most realms (over 70% in all cases). Different structural factors appear to control carnivore communities in the tropical and temperate latitudes of the Earth. Carnivore community structure in the Holarctic realms is conditioned by the Pleistocene glaciations, together with the presence of physical barriers. Furthermore, in the tropical realms, the main structural factor involves communities' high ecological diversity. Therefore, despite observing a major modulating role of biogeography and macroclimatic changes, we have succeeded in confirming a relationship between the environment and the community structure of carnivore faunas.

Introduction

Ecological groups can characterize ecosystem dynamics and community relationships, a fact that enables us to classify natural information in comparable units. During the last few decades, numerous terms have been employed to define these groups, and definitions overlap, but two of them come to the fore: ”guild” and “functional group” (Salt 1957, Root 1967, Simberloff & Dayan 1991, Lavorel & Garnier 2002, Menge *et al*. 1986) are usually used as equivalents, and refer to a group of species that overlaps with regard to resource requirements and obtains them in a similar way.

Over the last century there have been several studies of functional groups involving plants (e.g. Root 1967, Smith *et al*. 1997), detritic benthic marine organisms (e.g. Turpaeva, 1953), vertebrate and invertebrate aquatic animals (e.g. Covich *et al*. 1999) or birds (e.g. Salt 1957). There have also been studies of terrestrial mammal ecology based upon this methodology (e.g. Van Valkenburgh 1985, 1989, Morlo 1999). Additionally, the relationship between mammal community structure and environment has been established in modern studies (e.g. Andrews *et al*. 1979, Reed 1998, Hernández Fernández *et al*. 2006, Terry *et al*. 2011). Functional groups, as the basic building blocks of communities, may therefore permit us to reveal other factors not directly associated with species composition, such as climate (Terborgh & Robinson 1986, Simberloff & Dayan 1991, Rodríguez *et al*. 2006).

Body Size Categories
Mega-predators
Large predators
Medium predators
Small predators
Micro-predators
Hunting Locomotor Behaviour
Cursorial predators
Ambulatory predators
Scansorial predators
Arboreal predators
Fossorial predators
Aquatic predators
Feeding Habits
Hipercarnivorous predators
Meat-bone eater predators
Carnivorous predators
Omnivorous predators
Insectivorous predators

Table 4.1.

Ecomorphological factors. Categories used to define the carnivore functional groups.

The main goal of the present research is to classify carnivore mammal fauna into groups according to their ecological features, with the aim of developing a useful tool for defining mammal predator community structure. Moreover, we will analyse the existence of a possible a relationship between climate and predator community structure in different localities.

Material and methods

Functional groups definition

In order to define the above mentioned carnivore

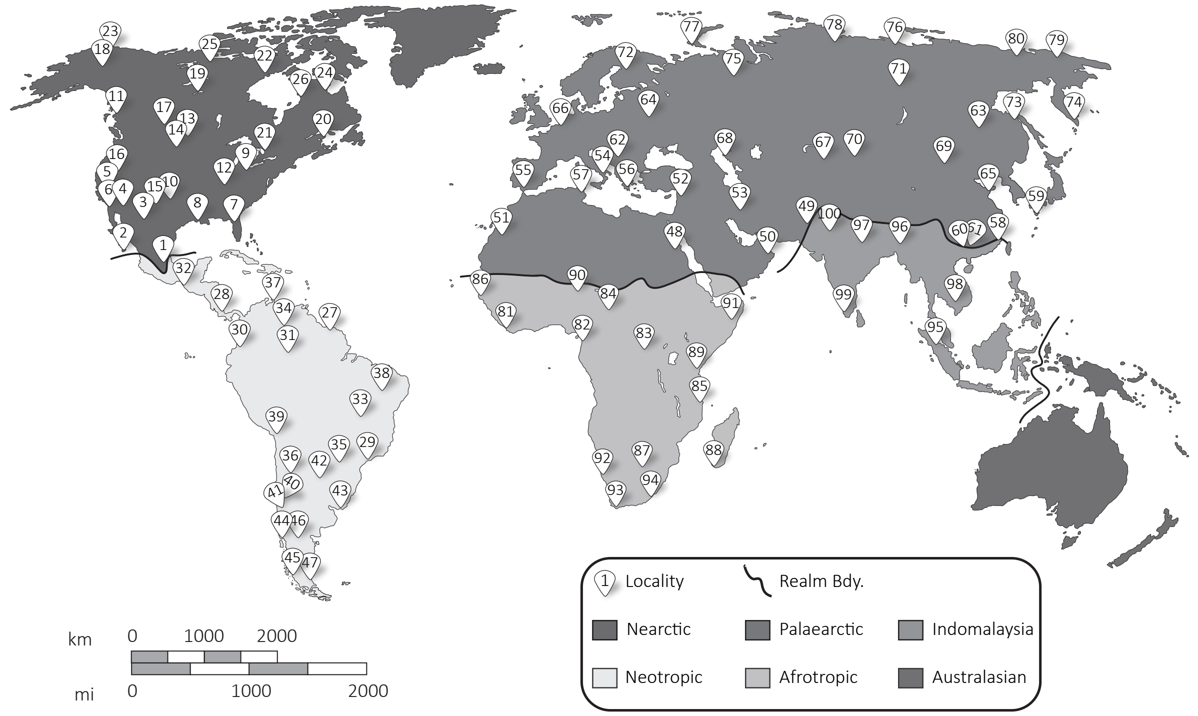

Figure 4.1. *Geographical distribution of the 100 communities analysed in the present research.*

functional groups, all terrestrial species of the order Carnivora (250 species, Wilson & Reeder 2005) were included in our analysis. This dataset included species that became extinct in historical times, but excluded three families of marine carnivores (families Odobenidae, Otariidae and Phocidae).

We combined three ecomorphological factors of the predator species (table 4.1, supplementary data 4.1) in order to obtain the Carnivore Functional Groups (CFG): body size categories (modified from Andrews *et al*. 1979 and Hernández Fernández *et al*. 2006), hunting locomotor behaviour (modified from Taylor 1974 and Van Valkenburgh 1985) and feeding habits (modified from Van Valkenburgh 1988 and Friscia *et al*. 2006).

We based the definition of the carnivore functional groups (CFG) upon a cluster analysis of all the species according to these three ecological variables. In order to obtain a dissimilarity matrix, and since the dataset includes both an ordinal variable -weight- and nominal factors -diet and locomotor strategies-, we applied the Gower distance (Gower 1971), as implemented in the R package cluster (R Development Core team 2012), which allows us to take advantage of the particularities of both kind of variables (nominal and ordinal). We subsequently obtained a cluster from this matrix using the *average* option in the function *hclust*.

Community analysis

Once each carnivore species had been classified into one functional group, we used faunal and climatic data from 100 modern continental localities distributed throughout the world, excluding Australia (fig. 4.1, appendix 1), to establish their community structure. We defined the carnivore functional spectrum as the sum of species included in each group converted to percentage. We conducted one-way ANOVA and Tukey and Games-Howell's post-hoc test (depending on the homogeneity of the variances marked for the Levene's test) in order to establish a relationship between any particular functional group and the different biomes present on Earth today (supplementary data 4.2, supplementary figure 4.1). We finally performed a discriminant function analysis (DFA) to determine the relationship between the carnivore community structure, represented by its functional spectra, and the biome of these localities. This analysis creates some discriminant functions by linearly combining every CFG's value and, afterwards, use those functions to test its prediction capacity on known climatic conditions (type of biome) of every locality. Consequently, when the predicting power of the functions was good, we used these functions in order to predict the unknown climatic condiciotns associated to a particular functional spectrum.

Apart from the global analysis, we repeated discriminant function analyses (DFA) and ANOVA tests, separating the localities according to biogeographic realms in order to determine the possible effects of the different evolutionary histories (Rodríguez *et al*. 2006, Cantalapiedra *et al*. 2013) upon the structure of the carnivore mammal communities and on the relationship between this and the environment. This process involved removing the cases belonging to biomes represented by only one community in each biogeographic realm, a procedure that reduced the climatic variability in some of the regions analysed. Consequently, in those few cases (Indomalaysian region) where only two biomes were represented, we applied for a t-Student and Levene's tests for equality of variances instead of the ANOVA and Tukey's post-hoc tests.

Results

Carnivore Functional Groups (CFG)

Eleven carnivore functional groups were obtained from the cluster analysis based on the ecological factors studied herein (fig. 4.2, supplementary figure 4.2).

- CFG 1: Comprising six species, it includes almost all cursorial predators, excluding the carnivorous species *Canis adustus*, and is mainly formed by medium-to-mega hipercarnivores. The cursorial meat/bone eater species *Crocuta crocuta* is also included here. Since this is the most differential group when compared to the others, it is the first group of species to be classified in an independent category.

- CFG 2: All species included within this group (38) are insectivore predators presenting an ambulatory or fossorial locomotor behaviour pattern. Most members weigh less than 4 kg, excluding *Proteles cristata*, which is also included in this category, despite its larger body size (10 kg).
- CFG 3: The three species included in this group are the only aquatic ones with a carnivorous diet.
- CFG 4: With 71 species, this is the largest group, and includes all the species with a carnivorous diet and a non-aquatic locomotor behaviour pattern (mainly arboreal/scansorial and ambulatory predators).
- CFG 5: Only two meat/bone eater species, both large ambulatory hyenas (*Hyaena hyaena* and *H. brunnea*), are included in this group.
- CFG 6: As with the aquatic carnivores from CFG 3, the two species forming this group, *Neovison macrodon* and *Mustela lutreola*, present a particular locomotor behaviour pattern and a specific diet, a fact that makes them sufficiently dissimilar to constitute their own category.
- CFG 7: Comprising 56 species, this is

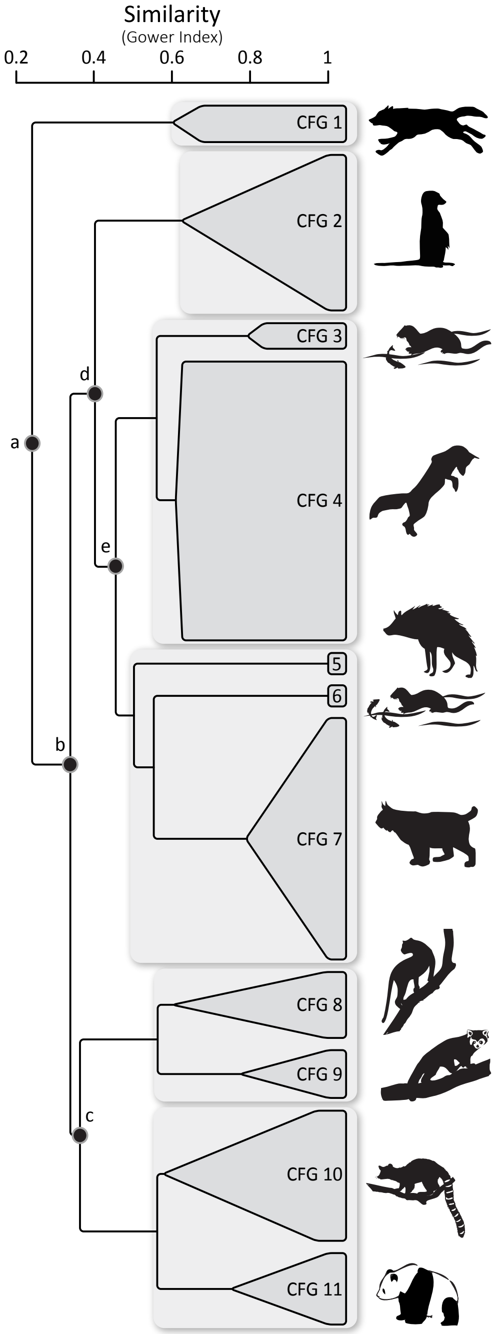

Figure 4.2. *Cluster showing the eleven carnivore functional groups obtained based on three ecological factors (body size, hunting locomotor behaviour pattern and feeding habits; supplementary data 4.1). We followed the taxonomy proposal from Wilson & Reeder 2005.*

the second largest group, made up of all ambulatory hipercarnivores, which are very heterogeneous with regard to body size.

- CFG 8: Although most of the 16 species constituting this group are scansorial with a hipercarnivorous diet, it also includes the coatis (*Nasua nasua*, *Nasua narica*) despite its insectivorous diet. Once again, this groups exhibits great variability in body size.
- CFG 9: All scansorial omnivores (10 species) are included in this group.
- CFG 10: This group includes all the omnivore species, excluding the scansorial and ambulatory ones (29 species).
- CFG XI: The17 species forming part of this category constitute the remaining ambulatory omnivores, and present a wide range of body sizes.

Intra-group similarity indexes (fig. 4.2) vary from 1 (CFG 5 and CFG 6 comprise species that exhibit exactly the same ecological features) to 0.58 (CFG 10 represents the group with the smallest similarity value). In view of the different ecological factors characterising the groups, the hunting locomotor behaviour and feeding habit appear to contribute to the clustering process to greater extent than body size, which would seem to determine the intragroup similarity degree.

Ecological meaning of the CFGs within the carnivore communities

The functional spectra from most communities are complex to analyse, with no particular functional group determining the ecological structure of any biome (supplementary data 4.3). Some of the functional groups, however, strongly characterise some biomes, a fact that is useful with regard to understanding the climatic boundaries reflected by the CFGs (fig. 4.3, supplementary figure 4.3 and supplementary data 4.4 resume the results of ANOVAs and t-Student test for the global and biogeographic realms analyses at a significance level below 0.05, and graphically show the distribution of the data).

The cursorial species from CFG 1 mainly separates open environments from forested ones in the Nearctic (figs. 4.3A), separating the tundra form the rest of biomes, excluding the tropical desert and the taiga. Similarly, CFG 2 characterises the functional spectra of the savanna and tropical desert communities in the Nearctic, as this group is only represented in these subtropical biomes in this biogeographical realm (fig. 4.3B).

Because of its strong correlation with the aridity and tree cover of the environment, the proportion of aquatic carnivores forming CFG 3, together with the representation of scansorial omnivores from GFC 9, separates the tropical rain forest

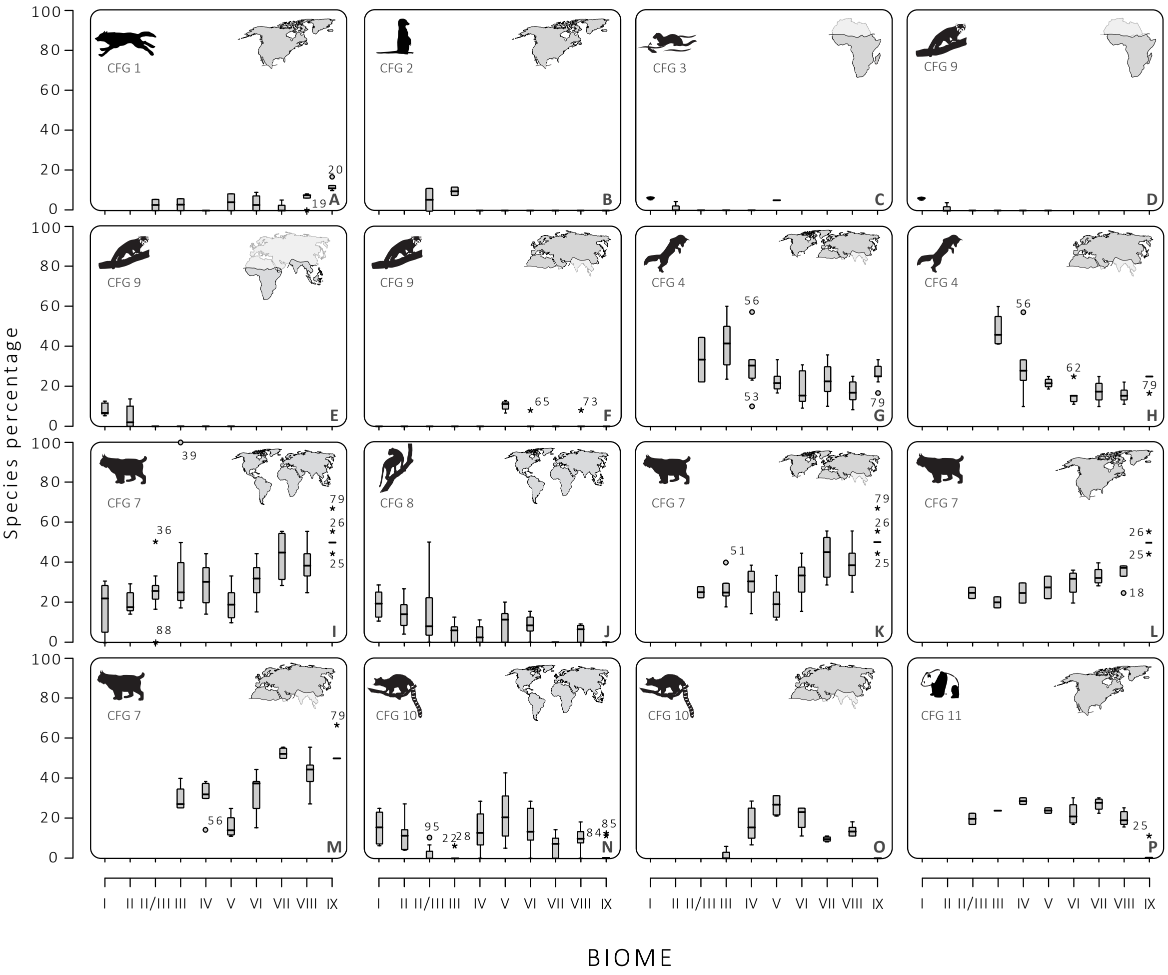

Figure 4.3. Graphical illustration of data distribution for the functional groups characterising biomes at global and biogeographical scale. Carnivore functional groups denoted as in figure 4.2 and main text.

from the remaining biomes in the Afrotropical realm (figs. 4.3C and 4.3D). CFG 9 also helps to discriminate the evergreen tropical rainforest from the savanna and the tropical desert in the Palaeotropics, and the temperate evergreen forest from the other biomes in the Palaearctic (figs. 4.3E and 4.3F). Because of their strong dependence on forest cover and food availability, the species forming this group are mainly present in the subtropical forested areas of the Palaearctic region, where tree cover is permanent and seasonal variations very low.

CFG 4 separates the clearly tropical environment of the tropical desert from the other temperate and cold biomes in the Palaearctic (fig. 4.3G). This pattern is also detected at the Holarctic scale, where this group separates the tropical desert from all other biomes except the savanna and sclerophyllous woodland-shrubland (fig. 4.3H).

Two functional groups separate biomes at global scale. While the proportion of ambulatory hipercarnivores from CFG 7 separates tundra from the rest of the biomes, except from steppe and taiga forest (fig. 4.3I), the proportion of scansorial hipercarnivores from CFG 8 separates the tropical rainforest from the temperate and arid subtropical biomes (fig. 4.3J). In temperate realms (Holarctic, Nearctic and Palaearctic), CFG 7 also separates the tundra from all the other biomes (figs. 4.3K-4.3M), excluding steppe, the taiga and/or tundra respectively (supplementary data 4.4). This group is represented in all biomes, but reaches its highest values in the coldest ones (biomes VII to IX).

At both, global and Palaearctic scale, CFG 10 separates open and dry biomes (tropical desert and/or tundra) from the rest of biomes, excluding the savanna (figs. 4.3N and 4.3O). Finally, the lack of ambulatory omnivores (GFC 11) in the tundra communities form the Nearctic enables this biome to be separated from all the others (fig. 4.3P).

It is worth pointing out that we encountered no relationship between the different functional groups and any biome analysed in the Indomalaysian realm (supplementary figure 4.3 and supplementary data 4.4).

Biome discrimination according to Carnivore Functional Spectra

Supplementary data 4.3 exposes the carnivore functional spectra for the modern localities and table 4.2 summarises the results of the different discriminant models.

At the global scale, this method has a low predictive power (table 4.2), with only 57% of correctly classified cases. The tundra and the evergreen tropical rain forest, however, obtained higher levels of correct classification in this discriminant analysis.

On considering the effect of the biogeographic history of the different faunas, a relevant improvement in results was observed. The analyses for Holarctic and Palaeotropic realms provided better results than global analysis; the predator community structure in particular shows a higher level of correlation with the different biomes in the Palaeotropics (94.4 % of correctly classified cases) than in the Holarctic (74.6 % of correctly classified cases). Whereas in the Holarctic only the savanna and tundra present all correctly classified cases, in the Palaeotropics almost all cases from most biomes were correctly classified (table 4.2).

This correlation between climate and predator community structure, which is stronger in the tropics than in temperate regions of the world, is also detected on analysing the results for the different biogeographic realms (table 4.2). While predictive percentages of over 94% are reached in all tropical biogeographic realms (Neotropics, Afrotropics and Indomalaysia), lower percentages (around 80%) of correctly classified cases are reached in the temperate regions (Nearctic and Palaearctic).

				BIOME									
	MODEL	N_L	%	I	II	II/III	III	IV	V	VI	VII	VIII	IX
	GLOBAL	100	57	90	40	30	50	60	60	0	70	70	100
	HOLARCTIC	59	74.6	-	-	100	66.7	62.5	83.3	55.6	87.5	50	100
	PALAEOTROPICS	18	94.4	100	83.3	100	100	-	-	-	-	-	-
BIOGEOGRAPHIC REALMS	NEARCTIC	26	80.8	-	-	50	100	100	100	50	100	60	100
	NEOTROPIC	19	94.7	100	100	66.7	100	-	100	-	100	-	-
	PALAEARCTIC	33	81.8	-	-	-	100	83.3	100	60	100	40	100
	AFROTROPIC	12	100	100	100	100	100	-	-	-	-	-	-
	INDOMALAYSIA	5	100	100	100	-	-	-	-	-	-	-	-

Table 4.2. *Summary of the eight models obtained for the discriminant analyses performed at global scale and according to biogeographical realms. NL, number of localities included in the analysis; %, percentage of correctly classified cases in the discriminant analysis.*

In temperate realms, temperate deciduous forest and taiga biomes systematically failed the inferences. In the Nearctic, additional misclassifications refer to the savanna, the temperate deciduous forest and the taiga (table 4.2). Whereas 50% of the cases were misclassified in the savanna and temperate deciduous forest, 40 % of the taiga communities from the Nearctic were misclassified. With the worst results of all biogeographic realms, 19.2 % of misclassified cases from the Palaearctic corresponded to seven communities from three biomes (table 4.2): sclerophyllous forest (1 community), temperate deciduous forest (2 communities) and taiga (3 communities).

On the contrary, most tropical communities from all biogeographic realms were correctly classified.

Discussion

Ecological implications of the Carnivore Functional Groups

Every functional group associates different carnivore species according to particular ecological features. While feeding habit and/or locomotor behaviour of their member species characterise all functional groups, body size category is more specific to two particular groups, CFG 6 (aquatic micro-hipercarnivores) and CFG 5 (bone-crusher hyeaenids). This is likely a consequence of the body size limitation that these kinds of locomotor and feeding behaviours present. While feeding habits appear to be the main factor contributing to separating the species into the different groups, locomotor behaviour defines intra-group variability. For example, CFG 2 and

CFG 10 are categorised by the feeding behaviour of its members (insectivore and omnivore species respectively) but, whereas CFG 2 can be divided into 2 subgroups according to locomotor behaviour, CFG 10 can be broken down into 3 subgroups, because the locomotor strategies developed by its members are more variable (supplementary figure 4.2). Finally, body size regulates the similarity degree between all species within each group.

The relevance in the clustering process of feeding behaviour in comparison to the rest of the ecological features analysed might be a consequence of the relationship between the amount of energy obtained by the predator and its type of dietary behaviour. Feeding habits of mammalian carnivores primarily determine the energy gained by the organism, as well as most of their ecology, including hunting behaviour, resting needs or breeding strategies (McNab 1986, 1989, Muñoz-García & Williams 2005). Furthermore, because of their dependence on prey availability, carnivores usually have large home ranges (McNab 1963, Kelt & Van Vuren 1999, Carbone *et al.* 2005), and spend a significant part of their energy on seeking and capturing prey (Garland 1983), which places hunting strategy as the second most important ecological factor influencing the clustering process.

Only CFG 1, the most dissimilar group comprising all cursorial predators except the carnivorous *Canis adustus* (the side-striped jackal), along with groups CFG 8 and CFG 9, are characterised by the locomotor behaviour of their members. This is probably a consequence of the high level of specialization that these types of locomotion require, with a higher energy cost resulting from the increase in chase speed in cursorial predators (Heglund & Taylor 1988) or the reduction, in most of cases, of muscle mass and metabolic basal rate to enable the animals to climb trees (McNab 1989).

Climatic restrictions on predator ecology and biogeographic implications of the Carnivore Functional Groups

As previously shown, some functional groups are closely related to several biomes in carnivore communities, particularly evergreen tropical rain forest, sub-tropical desert, temperate evergreen forest and tundra.

The common ecological pattern detected in the tundra communities of the northern biogeographic realms can be explained as a consequence of the biogeographical implications of the Pleistocene glaciations and the effect that this extreme climate has on its predator community structure (supplementary data 4.3). The mammal fauna dispersed from holarctic realms through the Bering land bridge established during the Pleistocene glaciations, which facilitated the sharing of a high number of species between the Palaearctic and the Nearctic. However, in such cold and open landscapes, where thermal seasonality is high and species must adapt their diet to the lack of food in winter, not all species can survive. The tundra landscape, dominated by bushy vegetation (shrubs, mosses and grasses), which basically supports small insects and flying animals, enables survival of migratory or small herbivores, such as lemmings, voles, squirrels, arctic hares and caribou (Chernov 1985, UCMP Team 2013). Additionally, the tundra biome is characterised by partially or permanently frozen soils (permafrost), which hamper the existence of fossorial species. Consequently, only terrestrial predators with a carnivorous or hipercarnivorous diet are able to survive in these regions (CFG 1 and CFG 7). Although the ambulatory hipercarnivore species included in CFG 7 are as common as ambulatory carnivores (included in CFG 4) in the temperate biomes of the world, the latter are not differentially distributed in tundra regions, while the CFG 7 species are statistically over-represented in this biome throughout (figs. 4.3I and 4.3K-M). A particular case of the dietary limitations imposed by the tundra can also be seen in the representation of ambulatory omnivores (CFG 11) in the Nearctic tundra (fig. 4.3P). While present in the other biomes of the bioregion, ambulatory omnivores are almost totally absent in the tundra communities analysed herein. Just one species, Ursus arctos, is found in some tundra communities in the region, and its capacity to inhabit these arctic environments would is likely related to its seasonal dietary behaviour and its hibernation capacity.

Predator community structure in evergreen tropical rain forest also seems to be highly conditioned by the particular features of this biome. In forest habitats with dense plant cover and high terrestrial prey biomass (Eisenbergh et al. 1979, Emmons et al. 1983), the ability to hunt or take cover in trees entails a substantial predatory advantage (Van Valkenburgh 1985). Consequently, the functional groups in which arboreal or scansorial locomotor behaviour governs the locomotion of its members should be well represented in this kind of biomes. While the strictly arboreal species are included in some groups characterised by their dietary behaviour and not by their locomotor strategy, the species in CFG 8 and CFG 9 represent almost all the scansorial predators. These groups reach the highest percentages in evergreen tropical rainforest globally (fig. 4.3J), in the Afrotropics (fig. 4.3D) and the Palaeotropics (fig. 4.3E), respectively, and characterise this biome together with some forested to semi-forested biomes (tropical deciduous forest, savanna and temperate evergreen forest).

CFG 3 also characterises the Afrotropical rainforest community structure (fig. 4.3D) because of the presence of Lutra maculicollis. Highly reliant on water availability, this species only inhabits clean freshwater habitats with permanent availability of water (Lariviere & Jennings 2009) and is distributed throughout all continental rainforests and the humid parts of tropical deciduous forests, but is absent from the rest of the Afrotropics.

Tropical desert and temperate evergreen forest also exhibit a correlation with some functional groups, but mostly at the biogeographical realm scale.

CFG 9 values in Palaearctic temperate evergreen forest are higher and statistically different from those of the other biomes (fig. 4.3F). Temperate evergreen forest is wetter, warmer and denser than most of the other biomes in this bioregion and can be considered as an equivalent to the tropical rainforest in temperate parts of the planet. Additionally, this biome presents a relatively low thermal and hydric seasonality; food, although seasonally conditioned, is available throughout the year, favouring species with a seasonal dietary adaptation (Hill 1997, Jayasekara & Takatsuky 2000). Consequently, predators with scansorial locomotion and an omnivorous diet (species from CFG 9) would encounter ecological benefits in this biome in comparison to other ones in the region.

CFG 2 and CFG 4, in turn, separate the tropical desert from other biomes in the Nearctic, Palaearctic and Holarctic.

The insectivore species in CFG 2, with their particular diet based upon large amounts of insects throughout the year, present tropical to subtropical distribution ranges and in the Nearctic are only present in the savanna and tropical desert biomes, being more common in the latter than in the former; thus, they are useful for separating the desert from other biomes (fig. 4.3C).

On the other hand, the overrepresentation of species from CFG 4 (including all the carnivorous species with any type of locomotion, excluding the aquatic ones) remains unclear. This functional group's proportion statistically differs between the tropical desert and all other biomes in the Palaearctics (fig. 4.3G), and with most of the biomes (excluding the savanna and the sclerophyllous woodland-shrubland) in the Holarctic (fig. 4.3H). Nevertheless, the ecological features characterising the species belonging to this group, with all carnivorous predators with a non-aquatic locomotion, do not represent particular adaptations to desert environments.

Finally, the omnivorous species form CFG 10 (fig. 4.3O) are underrepresented in both, tropical desert and tundra biomes, compared to the rest of biomes. All the species from CFG 10 are omnivores with an arboreal, aquatic or fossorial hunting locomotor behaviour. Its particular ecology, highly reliant on food availability throughout the year and forested conditions makes its survival virtually impossible in treeless and arid environments such as the tropical desert and the tundra.

Climate vs. Carnivore Functional Groups. Analyses of Global and Holarctic vs. Palaeotropic realms

Due to the physical and temporal isolation of their different communities, most biomes showed different patterns in the structure of their mammalian communities. However, two biomes, tundra and evergreen tropical rainforest, present a particular structural pattern that allows them to be climatically discriminated from the other biomes by means of their carnivore fauna. Although the effect of isolation is reduced on considering the biogeographic history of the different faunas, it exerts a different influence in the Holarctic and Palaeotropic realms. This is probably a consequence of the different structural effects of the Pleistocene glaciations upon the mammalian faunas in the northern *vs.* southern realms. Whereas in the Holarctic, only the communities of the Nearctic savanna and the tundra have all been correctly classified, most of the biomes have been correctly classified in the Palaeotropic region (table 4.2).

The tundra is a climatically and ecologically homogeneous biome with functional spectra common to all its localities, as a consequence of the relatively high percentage of species shared by all carnivore mammal communities in the tundra (20-50%). As was previously mentioned, a plausible cause of this similarity in faunas could involve the frequent land connections established between Siberia and Alaska during the Pleistocene (Simpson 1947, Hopkins 1959, Elias *et al.* 1996, Lozhkin *et al.* 2011). North American and Eurasian mammals were able to disperse between both continents through the Beringia land bridge, which homogenised the tundra faunas across the Holarctic region. This land bridge became a determinant factor in the structure and distribution of Holarctic terrestrial life (Cook *et al.* 2005), due to the availability of new niches for the immigrant species and especially for members of the order Carnivora, which are widely dispersed in space (Kelt & Van Vuren 1999, Jetz *et al.* 2004).

Moreover, although evergreen tropical rainforest has been globally discontinuous since the disruption of Gondwana, it presents a common community structure in relation to its carnivore functional spectra. Its habitat heterogeneity and species diversification rate are high (Pianka 1966, Rohde1992, Hernández Fernández & Vrba 2005, Cantalapiedra *et al.* 2011), a fact that favours development of specialized strategies for gaining available resources and reducing interspecific competitiveness (Evans *et al.* 2004). Nevertheless, these strategies are limited and tend to converge in the same kind of environment (community convergence) regardless of geographic region (Cody & Mooney 1978, Crowder 1980). The high diversity found in tropical biomes may be a consequence of the effects of high speciation and/or low extinction rates in the tropics, both related to the historical stability of this biome during long-term climate changes (Wallace 1878, Fischer 1960, Pianka 1966, Colinvaux *et al*. 2000), or to the forest contraction/expansion process associated with climate change, known as the refuge theory (Haffer 1982, Vrba 1995, Hernández Fernández & Vrba 2005, Moreno Bofarull *et al*. 2008). In any case, the species richness encountered in tropical forests enabled conservation of a community structure that would otherwise have been lost, endowing carnivore mammals with a common pattern for structuring their communities throughout the world, despite their different faunal compositions and geographic situations.

The Holarctic savanna communities, Santiago and Rio Verde, are the only representatives of this biome in the holarctic realms and are both located within a small region in the southern cone of North America. The structure of these communities, which share a substantial number of carnivore species (77.8% of the species from Santiago are also present in Río Verde), is highly influenced by species with a tropical to sub-tropical distribution, and clearly differs from the rest of the carnivore communities from other biome spectra in the Holarctic region (supplementary data 4.3).

Comprising the Afrotropical and Indomalaysian realms, the Palaeotropics have been environmentally continuous since the middle Miocene (Rögl 1999), connected by faunally diverse tropical forests and woodlands (Pickford & Morales 1994) and presenting a common basal community structure in the different biomes. The aridity increase through the Pleistocene glaciations, however, caused the expansion of savannas and deserts, gradually reducing forest dimensions (Cerling 1992, deMenocal 1995, Bobé & Behrensmeyer 2004, Hernández Fernández & Vrba 2006). Located in the north western extreme of the Afrotropical range of the tropical deciduous woodland, and closer to its limits with the northern savanna, Ziguinchor (Senegal) is the only case misclassified as savanna in the Palaeotropics. Highly influenced by neighbouring biomes, Ziguinchor's community shares a high number of species with the surrounding savanna and tropical deciduous woodland communities (82.6% with Zinder and Moundou; 72 % with Mtwara); but its community structure is closer to savanna because of the presence of *Hyaena hyaena*, an open-habitat dweller, adapted to arid and semiarid environments (Hofer 1998), which is also found in the savanna locality of Zinder. Climatic conditions in Ziguinchor enable hyenas to survive due to slightly dryer, and consequently less forested environments, in relation to other tropical deciduous forests ($D_{\text{Ziguinchor}}$ = 6.7 months; D_{Moundou} = 5.8 months; D_{Mtwara} = 5.5 months; D denotes annual drought length, see Hernández Fernández & Peláez-Campomanes 2005).

Climate vs. Carnivore Functional Groups. Analyses of biogeographic realms

Climate appears to be related to predator community structure in a complex manner, with no particular functional group characterizing the ecological structure of most biomes. It seems, however, that biome characteristics regulate predator community structure when biogeographic history is taken into account (table 4.2).

However, some cases constitute outliers of the biome pattern, and are of particular interest to us because they can shed light on the processes underlying the pattern observed. In the northern realms most misclassifications are associated with the temperate and cold biomes of the holarctic realms, which were deeply affected by the Pleistocene glaciations. Global cooling and aridification caused the development of climatic barriers (biomes) which blocked the faunal flow between communities of the same biome, favouring faunal interchange between the communities of nearby biomes across smooth ecotone climatic gradients. In some other cases, the main conditioning factor affecting the composition of faunas is the presence of a physical barrier (seas or mountains).

<u>*The glaciation effect*</u>

The Holarctic realms (Nearctic and Palaearctic) were deeply affected by climate changes on Earth during the Pleistocene, and this dramatically altered the environmental landscapes of these regions (Prentice & Jolly 2000, Whitlock *et al.* 2001), particularly in the temperate and cold biomes (Colinvaux *et al*. 2000, Markgraf & McGlone 2005). During this period, temperate evergreen and nemoral broadleaf-deciduous forests were constricted by global cooling, while the tundra, taiga and central steppes of North America and Asia expanded (Thompson & Anderson 2000, Ni *et al*. 2010). But the warming process associated with each interglacial stage reversed this process (Fredlund & Tieszen 1997, Ni *et al*. 2010). This climate change hampered species migration between the different nemoral broadleaf-deciduous forest domains that had previously developed during the Plio-Pleistocene glaciation (Potts & Behrensmeyer 1992), but favoured the mixture of species from other biomes such as taiga and temperate evergreen forest. This faunal mixture of species from neighbouring biomes was favoured in the northern latitudes of the holarctic realms, with a high percentage of the species shared by temperate evergreen forests, nemoral broadleaf-deciduous forests, steppe and taiga. Although differences in the faunal composition resulting from physiological constrictions of the species cause changes in the structure of the mammal communities, and enable biomes to be separated, some localities present a community structure similar to that of the neighbouring biomes because of the presence and/or absence of some species. This is the case of the several species in CFG 7 and CFG 8 in taiga and nemoral deciduous forests in the Holarctic realms. Some representatives of CFG 7 are absent from the taiga communities of Fairbanks and Kajaani, thus changing the community structure to a nemoral forest one, whereas some others, present in the nemoral broadleaf-deciduous forest communities of Cleveland and Vlissingen, change the structure of these communities to the taiga type. This correlation reflects the relationship previously established between CFG 7 and the coldest biomes (biomes VII to IX) in the Holarctic, where it reaches its highest values. On the other hand, the absence of scansorial species from CFG 8 in the Edmonton, Petropavlovsk and Erbogachen taiga communities changes the community structure to a steppe one. Finally, in the relatively poor nemoral broadleaf-deciduous forest communities of St. Louis and Tsingtao, and due to the percentage-base methodology employed in our analyses, the effects of the absence some particular species from CFG 7 alter the community structure to a temperate evergreen forest type.

The physical isolation effect

Most of the tropical biomes of the holarctic realms, as well as the tropical realms themselves, are distinguishable by their particular community structure. Two biomes, however, exhibit misclassified cases in some domains. In most of these cases, the main cause is the isolation of the domain from the rest of the biome due to the development of a physical or climatic barrier, together with the high faunal influence of the surrounding biome.

Santiago, in Baja California, is efficiently isolated from the rest of the continental domain of the savanna biome by the Sierra Juarez and San Pedro Mártir mountain ranges. This community is highly influenced by the carnivore fauna from the tropical desert, with all the fauna from Santiago also present in the nearby desert of Phoenix, whereas its faunal composition is very different from the other savanna community, Río Verde (only 38.9 % of the species from Río Verde are present in Santiago). It is worth pointing out that the faunal similarity between Nearctic tropical desert and savanna is masked when the Nearctic and Palaearctic realms are considered together as the Holarctic realm, because of the low community structure similarity of the different biomes of both realms. Thus, Rio Verde and Santiago, the only two savanna-type communities from the Holarctic, become sufficiently similar to present a common community structure that is different from that of the other biomes.

The sclerophyllous woodland community of Tunis is classified as tropical desert. In this case, the Mediterranean Sea acts as a barrier separating this community from the other sclerophyllous woodland communities studied herein (only 57.1% and 53.8% of the species from Sanlucar de Barrameda and Tripoli are present in the Tunis predator mammal fauna). Nevertheless, the carnivore community structure of Tunis shows the substantial influence of the nearby desert communities (80% and 87.5% of the predator species from Muscat and Assuan are also found in Tunis).

Finally, the savanna community of Remanso is climatically influenced by the surrounding Brazilian tropical deciduous forest and has the lowest aridity period of all savanna-type communities from the Neotropics ($D_{Remanso}$ = 6.9 months; $D_{Las\ Piedras}$ = 8.6 months; $D_{Catamarca}$ = 9.2 months). The limits of these two biomes are climatically smoothed and, because of the gradual transition between them, together with the lack of any physical barrier, woodland-dwelling species are able to move easily between both biomes. On the contrary, the savanna-type species from the rest of the savanna domains in the Neotropics are unable to cross the Brazilian forest, which acts as a climatic barrier for them. Consequently, due to the high influence of the species from the surrounding biome (all the fauna from Remanso is also present in Brasilia, the nearest locality in our analysis), the community structure of Remanso is closer to a tropical deciduous forest than to a savanna.

Conclusions

The ecology of carnivore mammals has been shown to be highly influenced by the environment. A relationship between carnivore community structure and climate can be established on taking into account the biogeographic history of the species. Although most of the carnivore communities were correctly classified when on considering their biogeographic history, in some cases errors were made in biome classification. This may be due to the influence of the Holarctic glaciations on Earth during the last 2.5 Ma. Additionally, the geographical isolation of different domains from the same biome has been shown to be another cause of alteration of the community structure of carnivore faunas.

In most cases, the capacity of carnivore functional spectra to discriminate among biomes is a function of the interaction among all carnivore functional groups, but in the tundra and the evergreen tropical rainforest, this pattern can be visually detected because of the strong correlation established between these biomes and some specific groups. Whereas in the tundra the Plio-Pleistocene glaciations constituted the main driving force helping to maintain community structure in cold environments, in tropical regions of the planet, it is the high ecological diversity of the tropical biomes that enables maintenance of a high species diversity that covered most of the available niches in these environments, allowing community structure to persist in time and space.

Finally, the present study has demonstrated the capacity of the carnivore functional groups to discriminate among biomes; this fact could lead to the development of new methodologies of environmental inference based on carnivore faunas. Although carnivores have usually been neglected in palaeoenvironmental studies, such methodologies might be useful for study of past environments associated with fossil sites presenting a rich carnivore assemblage.

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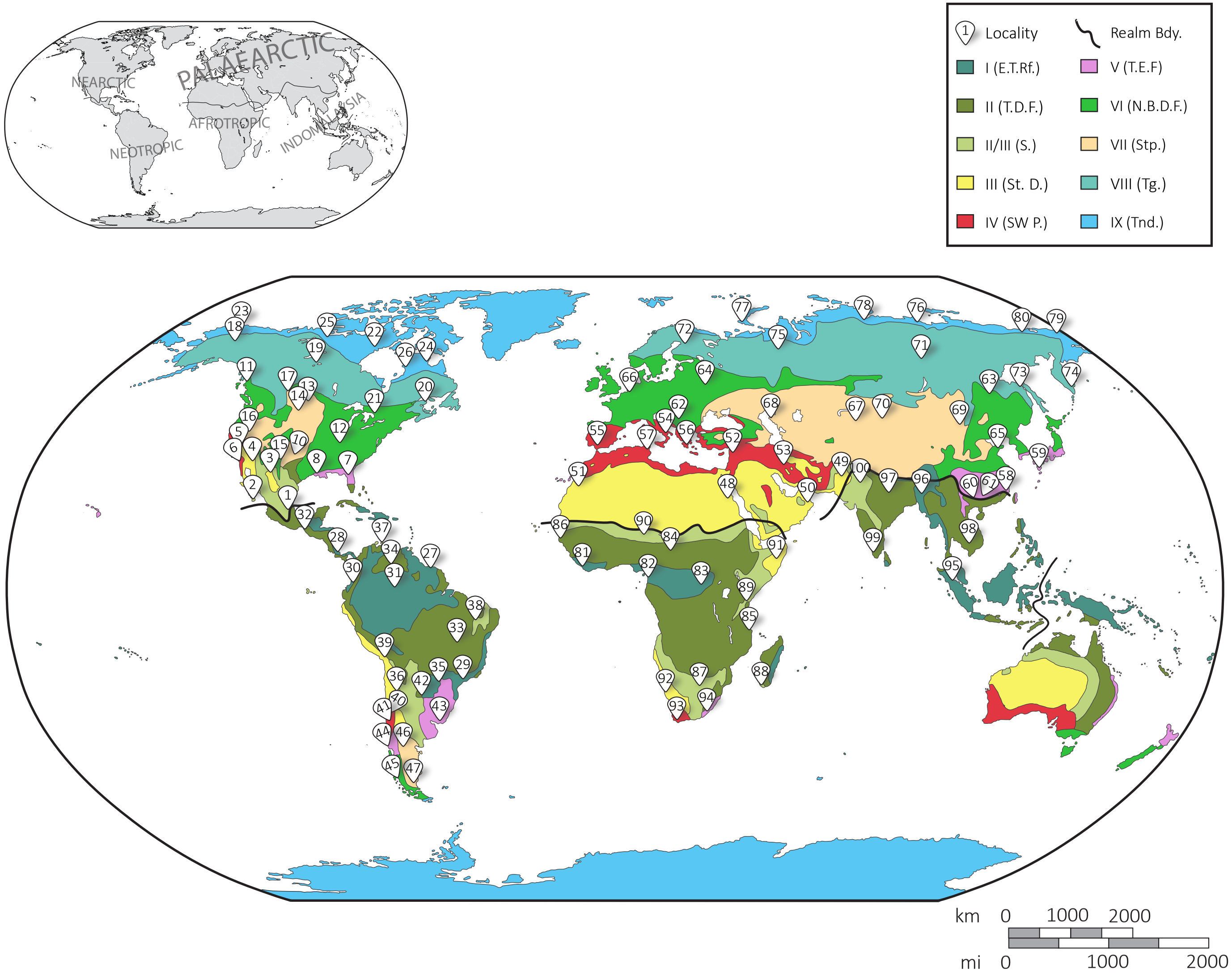
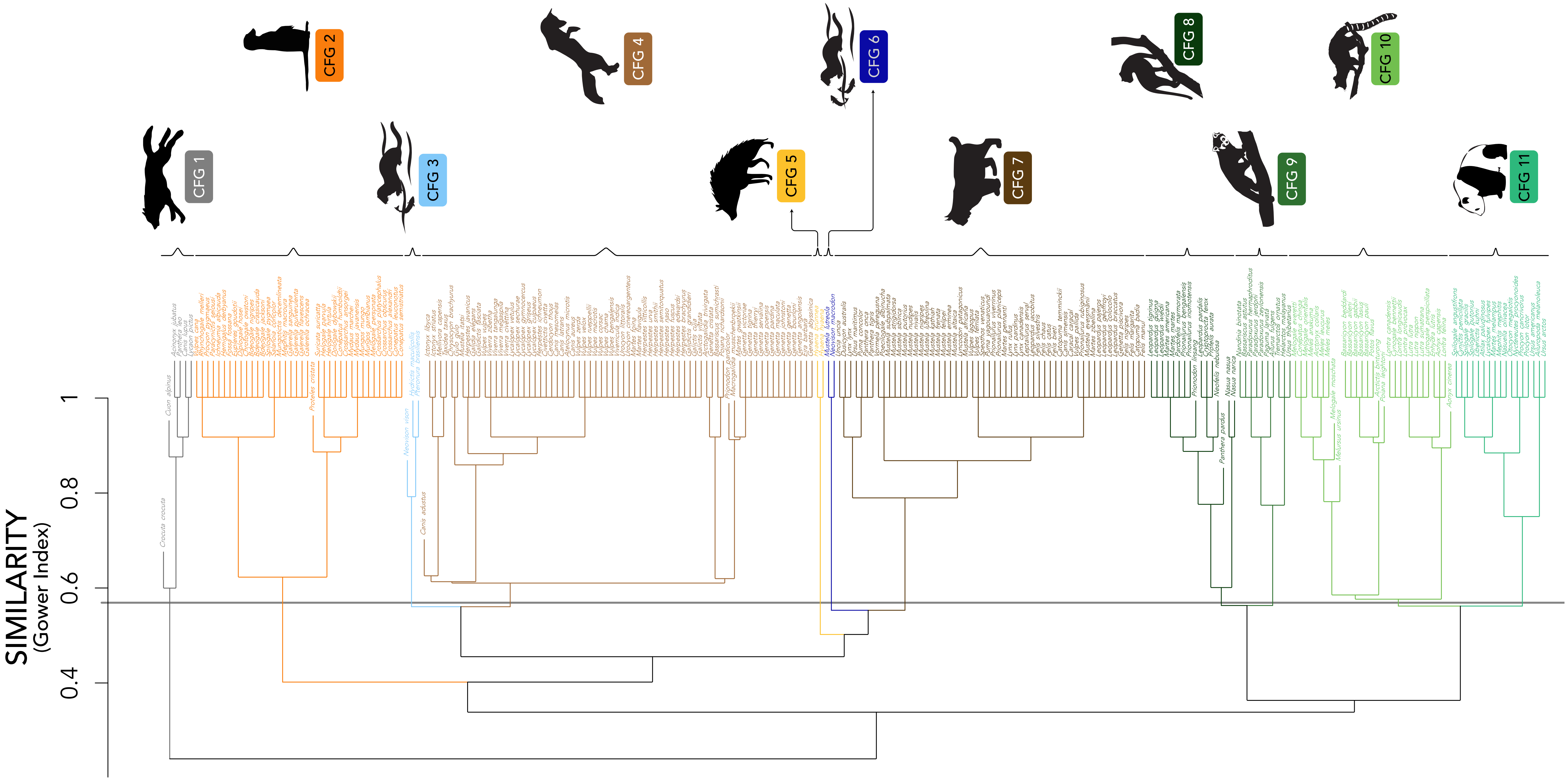
Supplementary data

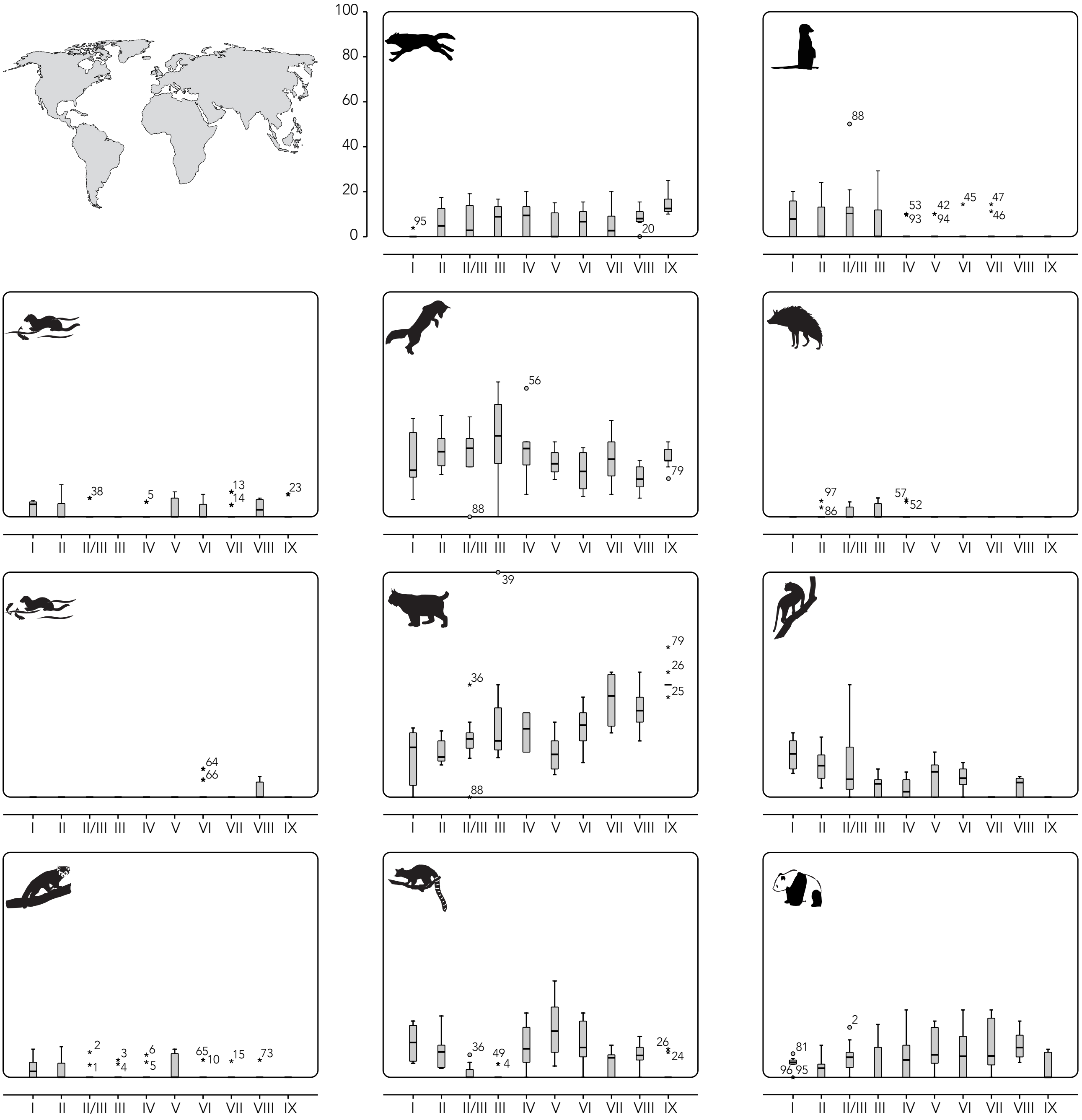
Supplementary figure 4.1. *Graphic and biomic situation of the 100 localitiesanalysed in this research. Biome typology as in supplementary data 4.2*



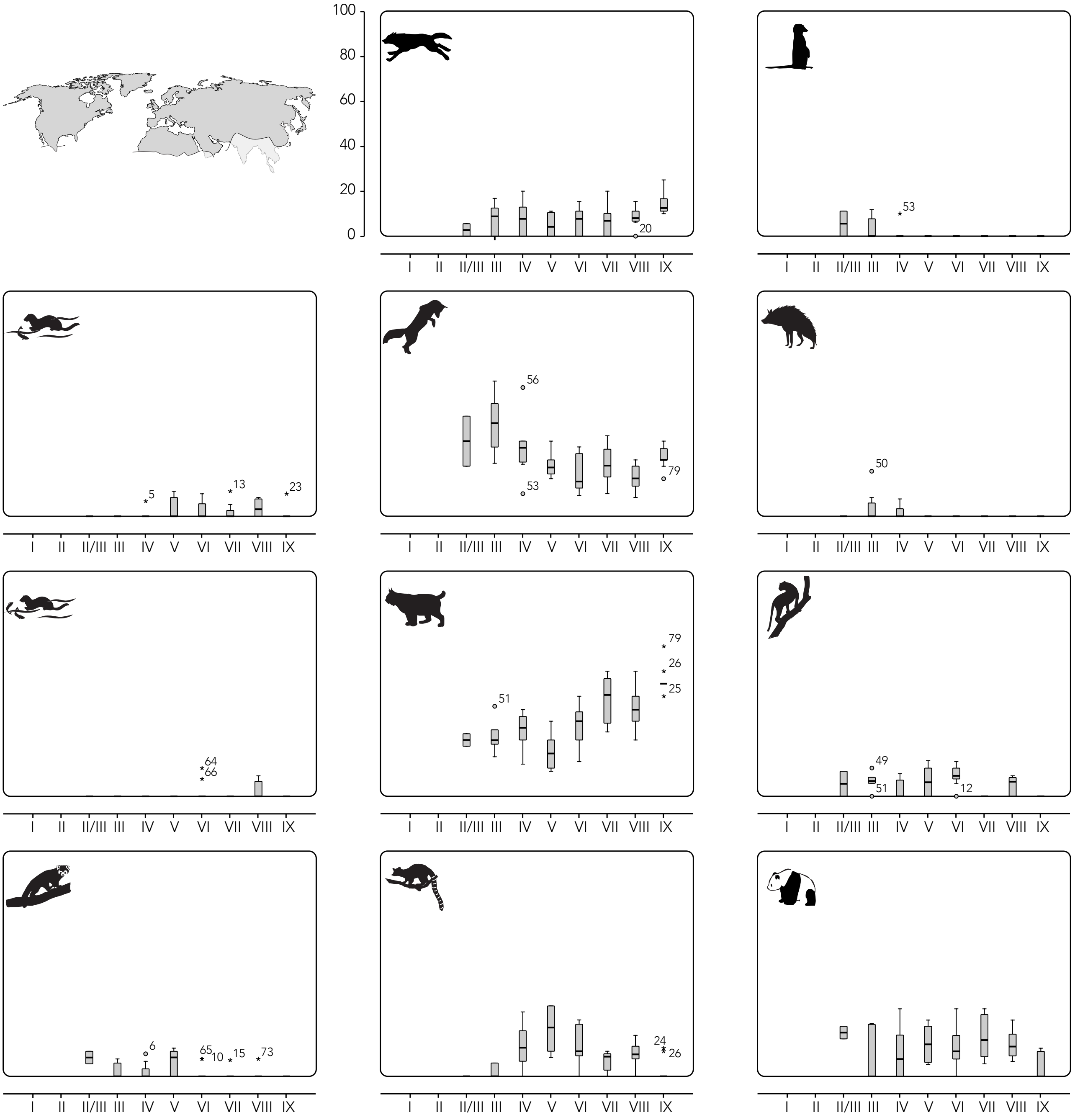

CFG 1
CFG 2
CFG 3
CFG 4
CFG 5
CFG 6
CFG 7
CFG 8
CFG 9
CFG 10
CFG 11
SIMILARITY
(Gower Index)
1
0.8
0.6
0.4

Supplementary figure 4.2. *CFG cluster (extended version). Cluster developed in this research showing the species association belonging to the different eleven functional groups.*

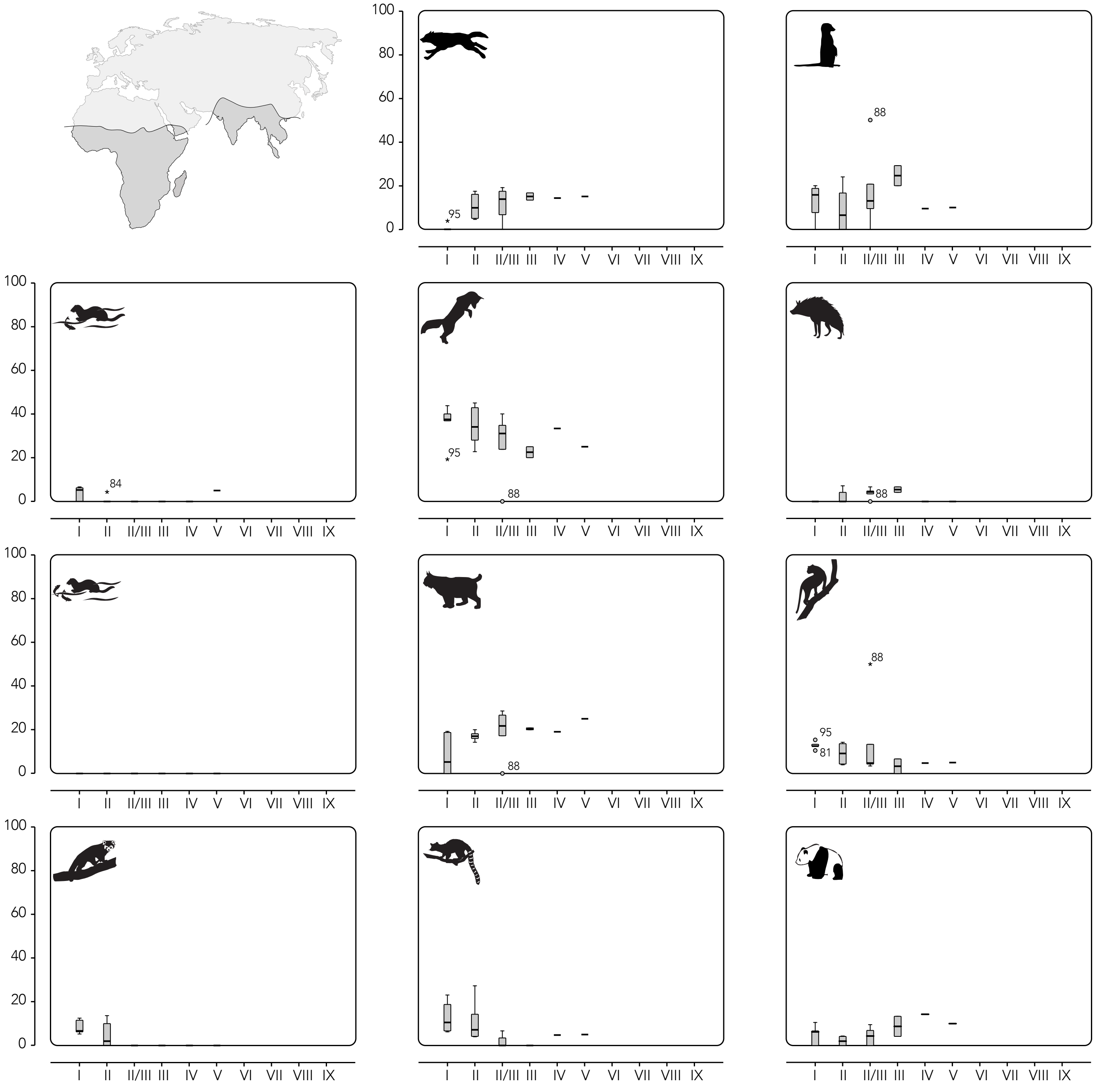
Supplementary figure 4.3. *Graphical illustration of the data distribution (extended version) of the eleven carnivore functional groups related to the ten biomes at global and biogeographical scale. Carnivore functional groups as in figure 4.2. Biome typology as in supplementary data 4.2.*



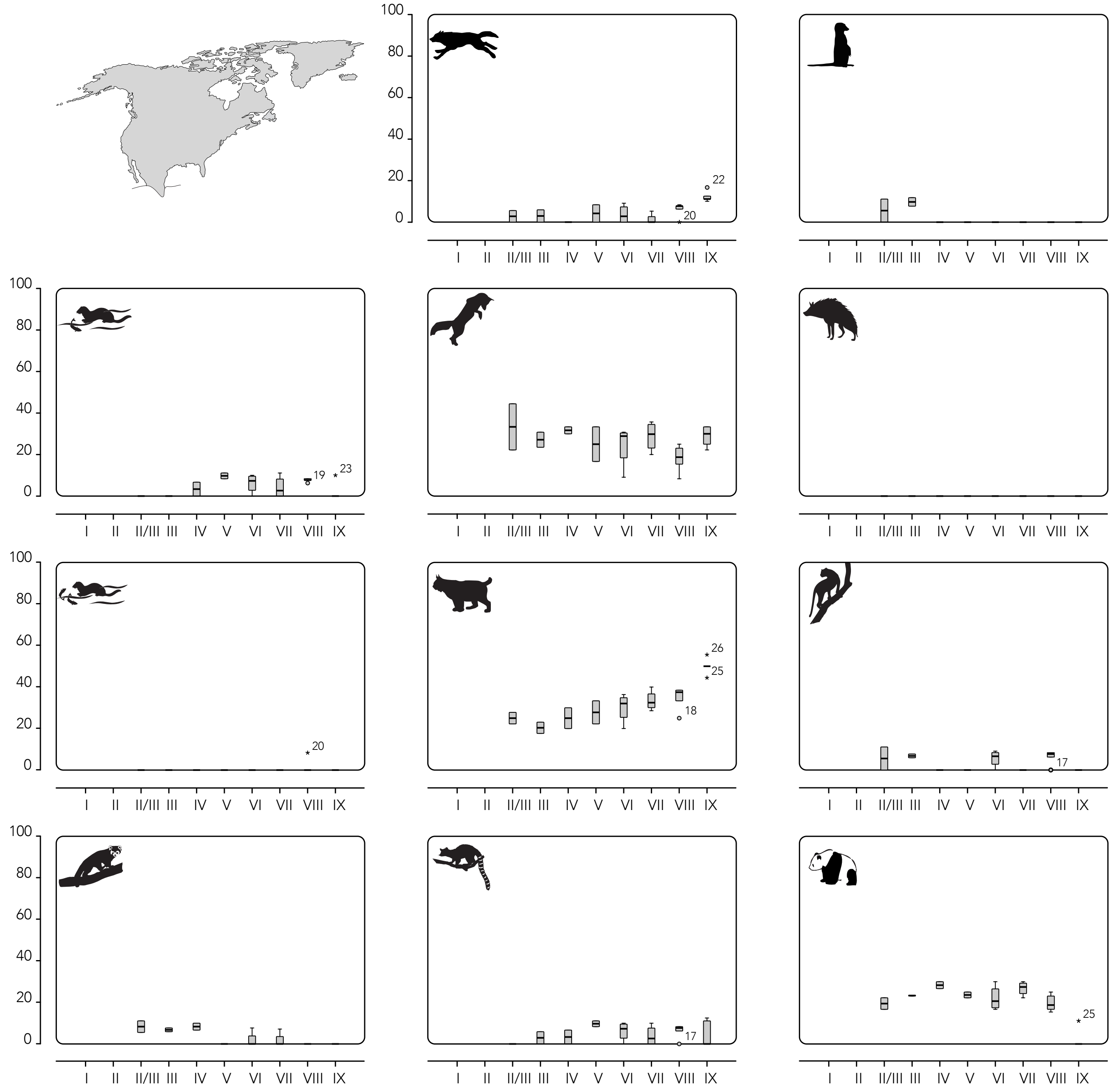
Supplementary figure 4.3. *Continued.*



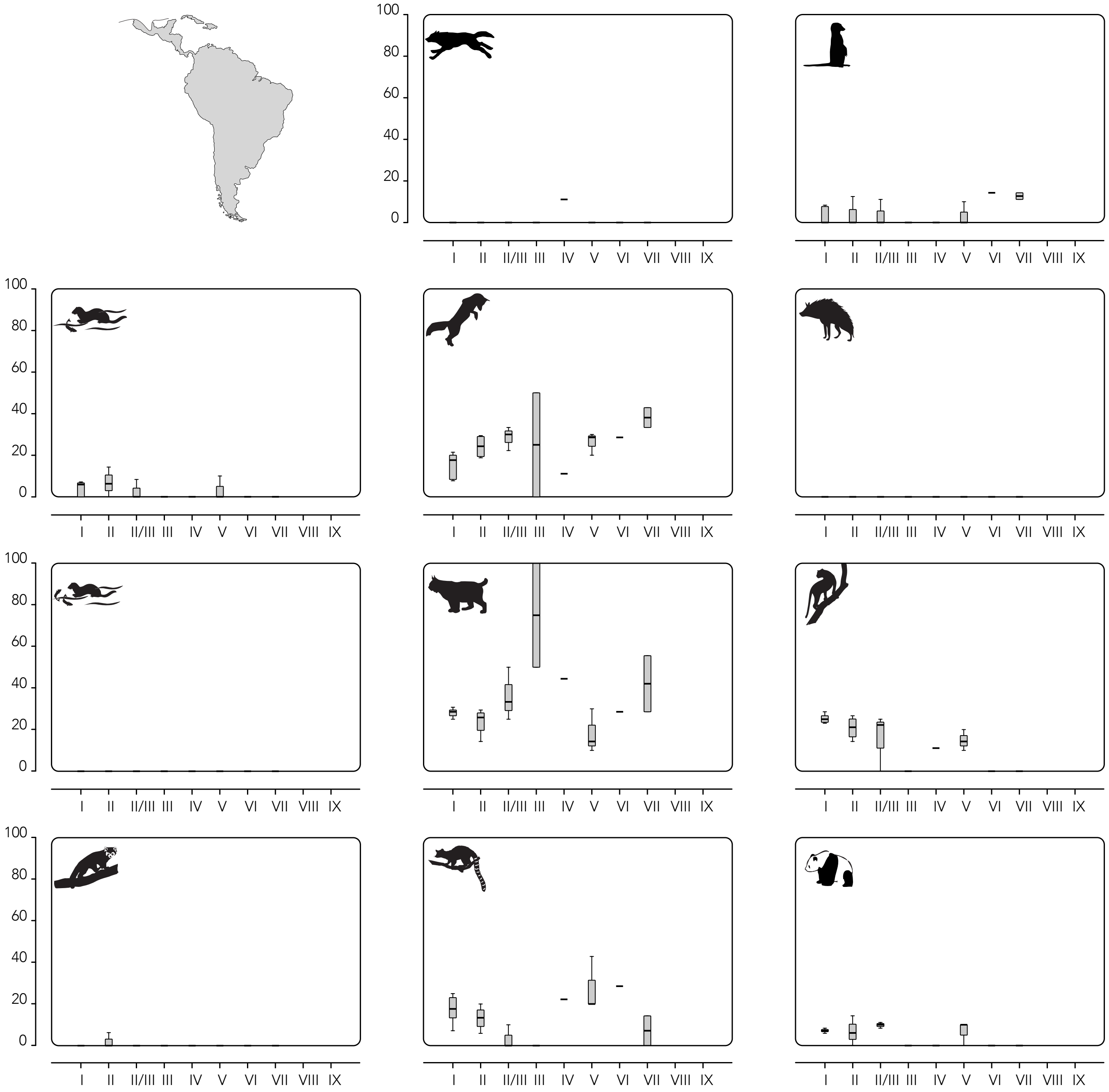
Supplementary figure 4.3. *Continued.*



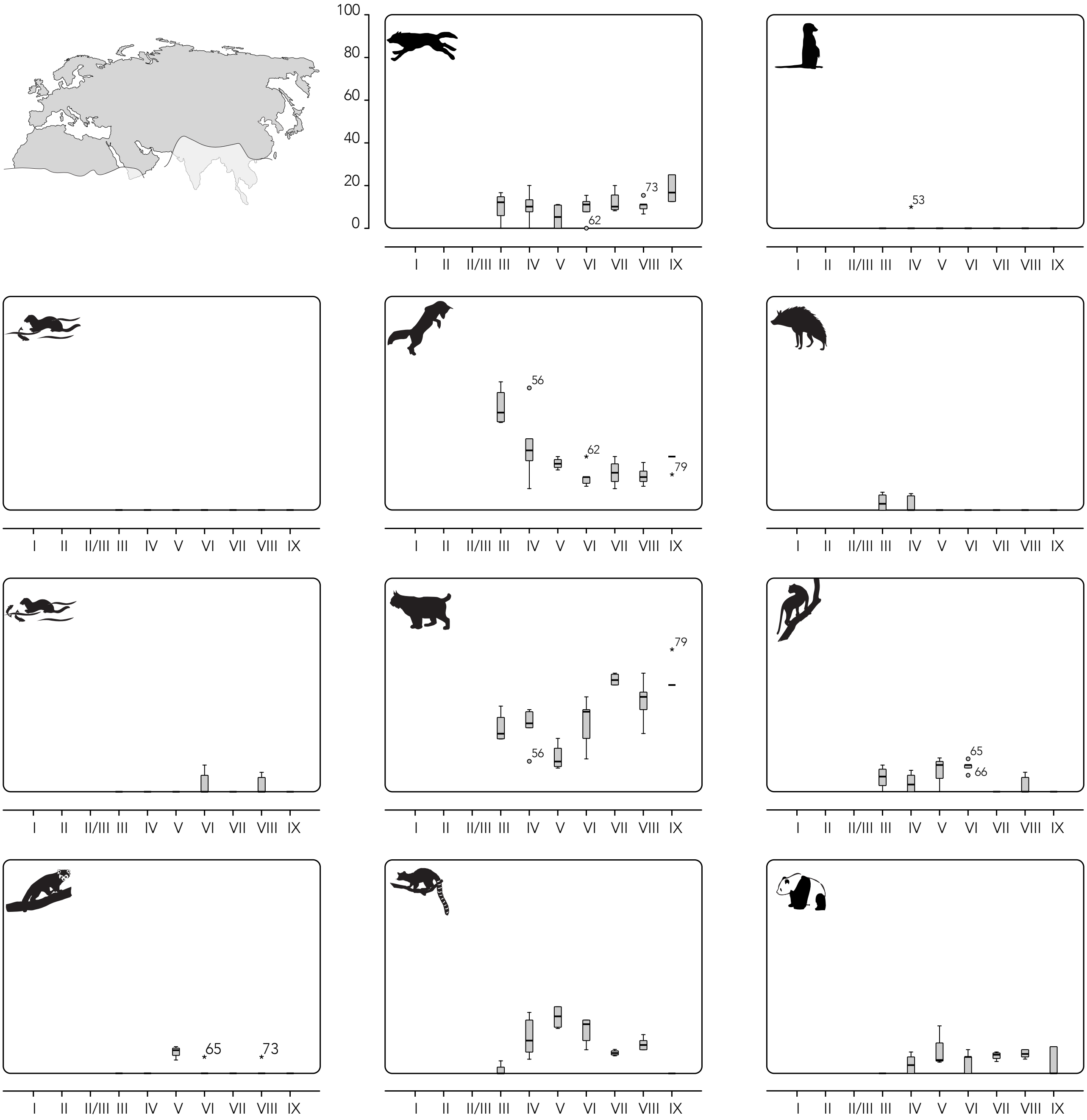
Supplementary figure 4.3. *Continued.*



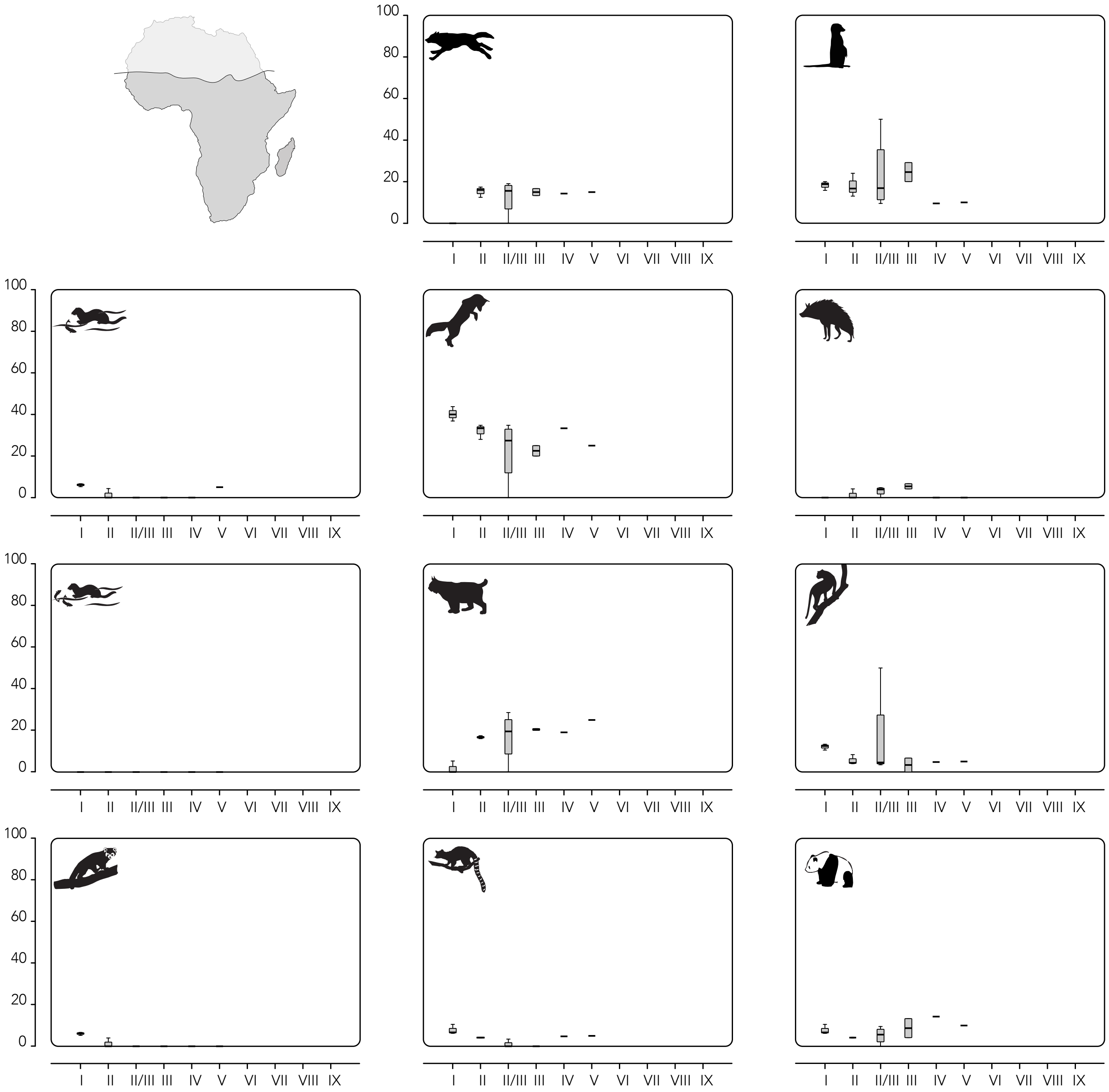
Supplementary figure 4.3. *Continued.*



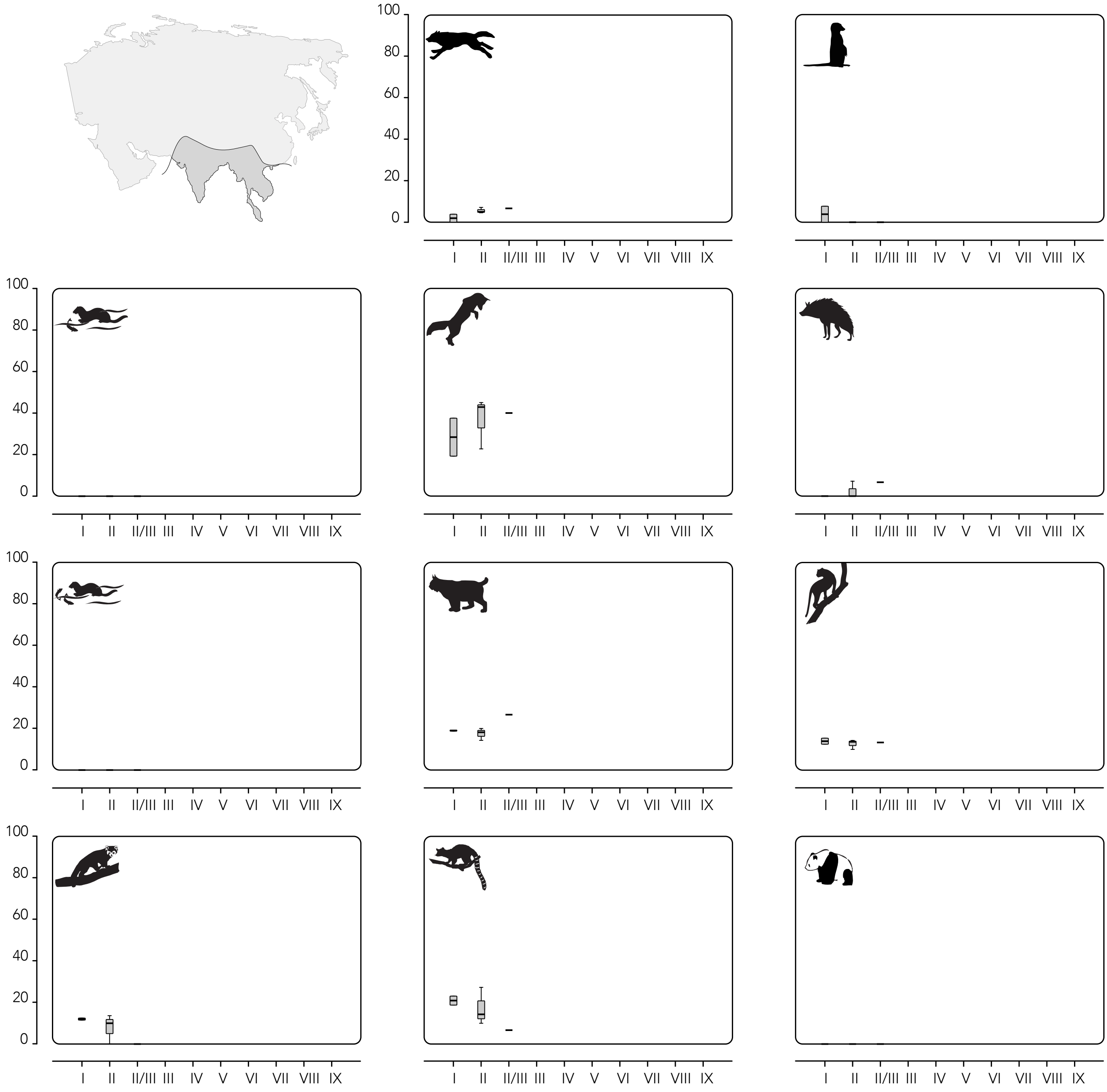
Supplementary figure 4.3. *Continued.*



Supplementary figure 4.3. *Continued.*



Supplementary figure 4.3. *Continued.*



Supplementary data 4.1. *Ecomorphological factors. Categories used combined to define the carnivore functional groups.*

	Body Size Categories
Mega-predators	Carnivore species larger than 45 kg.
Large predators	Carnivore species with a body size ranging between 15 to 44.9 Kg
Medium predators	Carnivore species with a body size ranging between 4 to 14.9 Kg
Small predators	Carnivore species with a body size ranging between 1 to 3.9 Kg
Micro-predators	Carnivore species smaller than 1 kg.
	Hunting Locomotor Behaviour
Cursorial predators	Carnivore species that rarely or never climb, developing a long distance chase and rarely preceded by a stalk.
Ambulatory predators	Carnivore species that rarely or never climb, with a short distance search (without chase), which ends in either a pounce or chase and sometimes preceded by a stalk.
Scansorial predators	Carnivore species capable of climbing, that usually climbs for escape.
Arboreal predators	Carnivore species that are rarely on the ground, living, foraging and taking shelters in trees.
Fossorial predators	Carnivore species that dig regularly for both, food and shelter.
Aquatic predators	Carnivore species that live and hunt in the water.
	Feeding Habits
Hipercarnivorous predators	Carnivore species that include more than a 70 % of meat in their diet.
Meat-bone eater predators	Carnivore species that include more than a 70 % of meat, with the addition of large bones, in their diet.
Carnivorous predators	Carnivore species that include 50-69.99% of meat in their diet.
Omnivorous predators	Carnivore species that include less than a 50 % of meat in their diet, with a large component vegetable matter and/or hard objects (mollusks or large crustaceans), as well as true omnivores for which no dominant food type could be discerned or species that mainly feed in vegetable matter.
Insectivorous predators	Carnivore species that include less than a 50 % of meat in their diet, with a dominion of invertebrates (mainly insects and chelicerates).

Supplementary data 4.2. *Climatic typology used in this research (following Walter 1970, Hernández Fernández 2001).*

Biome	Zonobiome (vegetation type)
I	Evergreen tropical rainforest
II	Tropical deciduous woodland
II/III	Savanna
III	Sub-tropical desert
IV	Sclerophyllous woodland-shrubland
V	Temperate evergreen forest
VI	Nemoral broadleaf-deciduous forest
VII	Steppe to cold desert
VIII	Boreal coniferous forest (taiga)
IX	Tundra

Supplementary data 4.3. *Carnivore functional spectra obtained for the 100 communities included in the analyses. Mp, corresponds to the number in map from figure 4.1 and appendix 1. ^{a}Cl., climate biome (classification as in supplementary data 4.2). R, represents the realm where the locality is allocated (1) Nearctic realm; (2) Neotropical realm; (3) Palaearctic realm; (4) Afrotropic realm; (5) Indomalaysian realm. N, is the number of carnivore species included in the locality. Carnivore functional groups labelled as in the main text.*

					CARNIVORE FUNCTIONAL GROUP (CFG)										
Mp	^{a}Cl.	R	Locality	N	1	2	3	4	5	6	7	8	9	10	11
1	II/III	1	Río Verde	18	5.6	11.1	0	22.2	0	0	27.8	11.1	5.6	0	16.7
2	II/III	1	Santiago	9	0	0	0	44.4	0	0	22.2	0	11.1	0	22.2
3	III	1	El Paso	13	0	7.7	0	30.8	0	0	23.1	7.7	7.7	0	23.1
4	III	1	Phoenix	17	5.9	11.8	0	23.5	0	0	17.7	5.9	5.9	5.9	23.5
5	IV	1	Fresno	15	0	0	6.7	33.3	0	0	20	0	6.7	6.7	26.7
6	IV	1	San Diego	10	0	0	0	30	0	0	30	0	10	0	30
7	V	1	Jacksonville	9	0	0	11.1	33.3	0	0	22.2	0	0	11.1	22.2
8	V	1	New Orleans	12	8.3	0	8.3	16.7	0	0	33.3	0	0	8.3	25
9	VI	1	Cleveland	18	5.6	0	5.6	27.8	0	0	33.3	5.6	0	5.6	16.7
10	VI	1	Colorado Springs	13	0	0	0	30.8	0	0	30.8	7.7	7.7	0	23.1
11	VI	1	Prince Rupert	11	9.1	0	9.1	9.1	0	0	36.4	9.1	0	9.1	18.2
12	VI	1	St Louis	10	0	0	10	30	0	0	20	0	0	10	30
13	VII	1	Medicine Lake	9	0	0	11.1	33.3	0	0	33.3	0	0	0	22.2
14	VII	1	Rapid City	19	5.3	0	5.3	26.3	0	0	31.6	0	0	5.3	26.3
15	VII	1	Santa Fé	14	0	0	0	35.7	0	0	28.6	0	7.1	0	28.6
16	VII	1	Winnemucca	10	0	0	0	20	0	0	40	0	0	10	30
17	VIII	1	Edmonton	13	7.7	0	7.7	23.1	0	0	38.5	0	0	0	23.1
18	VIII	1	Fairbanks	12	8.3	0	8.3	25	0	0	25	8.3	0	8.3	16.7
19	VIII	1	Fort Smith	16	6.3	0	6.3	18.8	0	0	37.5	6.3	0	6.3	18.8
20	VIII	1	Gaspé	12	0	0	8.3	8.3	0	8.3	33.3	8.3	0	8.3	25
21	VIII	1	Smoky Falls	13	7.7	0	7.7	15.4	0	0	38.5	7.7	0	7.7	15.4
22	IX	1	Baker Lake	6	16.7	0	0	33.3	0	0	50	0	0	0	0
23	IX	1	Barrow	10	10	0	10	30	0	0	50	0	0	0	0
24	IX	1	Cape Hope Advances	8	12.5	0	0	25	0	0	50	0	0	12.5	0
25	IX	1	Coppermine	9	11.1	0	0	33.3	0	0	44.4	0	0	0	11.1
26	IX	1	Port Harrison	9	11.1	0	0	22.2	0	0	55.6	0	0	11.1	0
27	I	2	Paramaribo	15	0	0	6.7	20	0	0	26.7	26.7	0	13.3	6.7
28	I	2	Puerto Limón	13	0	7.7	0	7.7	0	0	30.8	23.1	0	23.1	7.7
29	I	2	Sao Paulo	14	0	0	7.1	21.4	0	0	28.6	28.6	0	7.1	7.1
30	I	2	Tumaco	12	0	8.3	0	8.3	0	0	25	25	0	25	8.3
31	I	2	Uapes	17	0	0	5.9	17.7	0	0	29.4	23.5	0	17.7	5.9
32	II	2	Acapulco	16	0	12.5	0	18.8	0	0	25	18.8	6.25	12.5	6.3
33	II	2	Brasilia	17	0	0	5.9	29.4	0	0	29.4	23.5	0	5.9	5.9
34	II	2	Puerto Ayacucho	15	0	0	6.7	20	0	0	26.7	26.7	0	20	0
35	II	2	Roque Sáenz Peña	7	0	0	14.3	28.6	0	0	14.3	14.3	0	14.3	14.3
36	II/III	2	Catamarca	10	0	0	0	30	0	0	50	0	0	10	10
37	II/III	2	Las Piedras	9	0	11.1	0	22.2	0	0	33.3	22.2	0	0	11.1
38	II/III	2	Remanso	12	0	0	8.3	33.3	0	0	25	25	0	0	8.3

Supplementary data 4.3. *Continued.*

					CARNIVORE FUNCTIONAL GROUP (CFG)										
Mp	[a]Cl.	R	Locality	N	1	2	3	4	5	6	7	8	9	10	11
39	III	2	Arica	1	0	0	0	0	0	0	100	0	0	0	0
40	III	2	Mendoza	2	0	0	0	50	0	0	50	0	0	0	0
41	IV	2	Santiago de Chile	9	11.1	0	0	11.1	0	0	44.4	11.1	0	22.2	0
42	V	2	Corrientes	10	0	10	10	20	0	0	10	20	0	20	10
43	V	2	Montevideo	10	0	0	0	30	0	0	30	10	0	20	10
44	V	2	Puerto Montt	7	0	0	0	28.6	0	0	14.3	14.3	0	42.9	0
45	VI	2	Evangelistas	7	0	14.3	0	28.6	0	0	28.6	0	0	28.6	0
46	VII	2	Maquinchao	9	0	11.1	0	33.3	0	0	55.6	0	0	0	0
47	VII	2	Puerto Sta. Cruz	7	0	14.3	0	42.9	0	0	28.6	0	0	14.3	0
48	III	3	Assuan	8	12.5	0	0	50	0	0	25	12.5	0	0	0
49	III	3	Jacobabad	17	11.8	0	0	41.2	5.9	0	29.4	5.9	0	5.9	0
50	III	3	Muscat	5	16.6	0	0	41.7	8.3	0	25	8.3	0	0	0
51	III	3	Smara	5	0	0	0	60	0	0	40	0	0	0	0
52	IV	3	Aleppo	13	7.7	0	0	23.1	7.7	0	30.8	7.7	0	15.4	7.7
53	IV	3	Isfahan	10	20	10	0	10	0	0	30	10	0	10	10
54	IV	3	Potenza	8	12.5	0	0	25	0	0	37.5	0	0	25	0
55	IV	3	Sanlucar de Barrameda	13	7.7	0	0	30.8	0	0	38.5	0	0	15.4	7.7
56	IV	3	Trípoli	7	0	0	0	57.1	0	0	14.3	0	0	28.6	0
57	IV	3	Tunis	15	13.3	0	0	33.3	6.7	0	33.3	6.7	0	6.7	0
58	V	3	Fuzhou	19	10.5	0	0	21.1	0	0	15.8	15.8	10.5	21.1	5.3
59	V	3	Kagoshima	9	11.1	0	0	22.2	0	0	11.1	0	11.1	22.2	22.2
60	V	3	Pingnan	16	0	0	0	25	0	0	12.5	12.5	12.5	31.3	6.3
61	V	3	Shaoguan	16	0	0	0	18.8	0	0	25	12.5	6.3	31.3	6.3
62	VI	3	Belgrade	8	0	0	0	25	0	0	37.5	12.5	0	25	0
63	VI	3	Blagoveshchensk	18	11.1	0	0	11.1	0	0	44.4	11.1	0	11.1	11.1
64	VI	3	Moscow	8	12.5	0	0	12.5	0	12.5	25	12.5	0	25	0
65	VI	3	Tsingtao	13	15.4	0	0	15.4	0	0	15.4	15.4	7.7	23.1	7.7
66	VI	3	Vlissingen	13	7.7	0	0	15.4	0	7.7	38.5	7.7	0	15.4	7.7
67	VII	3	Almaty	18	11.1	0	0	16.7	0	0	55.6	0	0	11.1	5.6
68	VII	3	Fort Shevchenko	11	8.3	0	0	25	0	0	50	0	0	8.3	8.3
69	VII	3	Baotou	11	9.1	0	0	18.2	0	0	54.6	0	0	9.1	9.1
70	VII	3	Urumqi	10	20	0	0	10	0	0	50	0	0	10	10
71	VIII	3	Erbogachen	9	11.1	0	0	11.1	0	0	55.6	0	0	11.1	11.1
72	VIII	3	Kajaani	11	9.1	0	0	18.2	0	9.1	27.3	9.1	0	18.2	9.1
73	VIII	3	Nikolayevsk-on-Amur	13	15.4	0	0	15.4	0	0	38.5	0	7.7	15.4	7.7
74	VIII	3	Petropavlovsk	9	11.1	0	0	22.2	0	0	44.4	0	0	11.1	11.1
75	VIII	3	Serov	15	6.7	0	0	13.3	0	6.7	46.7	6.7	0	13.3	6.7
76	IX	3	Bulum	8	12.5	0	0	25	0	0	50	0	0	0	12.5
77	IX	3	Malye-Karmakuly	4	25	0	0	25	0	0	50	0	0	0	0
78	IX	3	Mys Chelyuskin	4	25	0	0	25	0	0	50	0	0	0	0
79	IX	3	Mys Shmidta	6	16.7	0	0	16.7	0	0	66.7	0	0	0	0
80	IX	3	Nizhnekolymsk	8	12.5	0	0	25	0	0	50	0	0	0	12.5
81	I	4	Greenville	19	0	15.8	5.3	36.8	0	0	5.3	10.5	5.3	10.5	10.5

Supplementary data 4.3. *Continued.*

					CARNIVORE FUNCTIONAL GROUP (CFG)										
Mp	[a]Cl.	R	Locality	N	1	2	3	4	5	6	7	8	9	10	11
82	I	4	Kribi	15	0	20	6.7	40	0	0	0	13.3	6.7	6.7	6.7
83	I	4	Yangambi	16	0	18.8	6.3	43.8	0	0	0	12.5	6.3	6.3	6.3
84	II	4	Moundou	23	17.4	13.0	4.4	34.8	0	0	17.4	4.4	0	4.4	4.4
85	II	4	Mtwara	25	16	24	0	28	0	0	16	4	4	4	4
86	II	4	Ziguinchor	24	12.5	16.7	0	33.3	4.2	0	16.7	8.3	0	4.2	4.2
87	II/III	4	Gaborone	21	19.1	9.5	0	23.8	4.8	0	28.6	4.8	0	0	9.5
88	II/III	4	Tulear	2	0	50	0	0	0	0	0	50	0	0	0
89	II/III	4	Voi	29	13.8	20.7	0	31.0	3.5	0	17.2	3.5	0	3.5	6.9
90	II/III	4	Zinder	23	17.4	13.4	0	34.8	4.4	0	21.7	4.4	0	0	4.4
91	III	4	Galcaio	24	16.7	29.2	0	25.0	4.2	0	20.8	0	0	0	4.2
92	III	4	Lüderitz Bay	15	13.3	20	0	20	6.7	0	20	6.7	0	0	13.3
93	IV	4	Cape Town	21	14.3	9.5	0	33.3	0	0	19.1	4.8	0	4.8	14.3
94	V	4	East London	20	15	10	5	25	0	0	25	5	0	5	10
95	I	5	Medan	26	3.9	7.7	0	19.2	0	0	19.2	15.4	11.5	23.1	0
96	I	5	Silchar	16	0	0	0	37.5	0	0	18.8	12.5	12.5	18.8	0
97	II	5	Patna	14	7.1	0	0	42.9	7.1	0	14.3	14.3	0	14.3	0
98	II	5	Phnom Penh	22	4.6	0	0	22.7	0	0	18.2	13.6	13.6	27.3	0
99	II	5	Trivandrum	20	5	0	0	45	0	0	20	10	10	10	0
100	II/III	5	Jaipur	15	6.7	0	0	40	6.7	0	26.7	13.3	0	6.7	0

Supplementary data 4.4. *Results for the ANOVA and Student t-test analyses on functional groups to separate biomes for global and biogeographic realms. Column 'F' lists the F-statistics for univariate analyses of variance (ANOVA) for that particular functional group between the different biomes. 'P' is the P-value for each comparison across all groups. Under each biome is listed the mean and standard deviation, in parentheses, for each functional group. 'Tukey and Games-Howell list significant differences between beiomes. Biomes as supplementary data 4.2.*

	CFG	F	P	Tukey/ Games-Howell	I	II	II/III	III	IV	V	VI	VII	VIII	IX
GLOBAL ANALYSES	1	3.831	< 0.001	I-VIII; I-IX; V-IX	0.385 (1.216)	6.258 (6.829)	6.245 (7.752)	7.681 (7.246)	8.661 (6.910)	4.497 (6.023)	6.133 (5.896)	5.380 (6.781)	8.333 (3.988)	15.306 (5.564)
	2	2.628	0.01		7.826 (8.002)	6.621 (9.079)	11.548 (15.283)	6.862 (10.421)	1.952 (4.118)	2.000 (4.216)	1.429 (4.518)	2.540 (5.406)	0.000 (0.000)	0.000 (0.000)
	3	1.633	0.118		3.787 (3.297)	3.118 (4.770)	0.833 (2.635)	0.000 (0.000)	0.667 (2.108)	3.444 (4.705)	2.465 (4.120)	1.637 (3.717)	3.830 (4.077)	1.000 (3.162)
	4	2.032	0.044	II-VIII; VIII-IX	25.242 (13.228)	30.343 (8.875)	28.185 (12.338)	34.214 (17.798)	28.710 (13.265)	24.060 (5.325)	20.559 (8.620)	26.140 (10.150)	17.078 (5.386)	26.056 (5.054)
	5	2.782	0.006		0.000 (0.000)	1.131 (2.485)	1.922 (2.602)	2.505 (3.385)	1.436 (3.037)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)
	6	2.529	0.012		0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	2.019 (4.405)	0.000 (0.000)	2.409 (3.923)	0.000 (0.000)
	7	8.325	< 0.001	I-VII; I-VIII; I-IX; II-VII; II-VIII; II-IX; II/III-IX; IV-IX; V-VII; V-VIII; V-IX; VI-IX; VII-IX; VIII-IX	18.366 (12.203)	19.789 (5.376)	25.255 (12.564)	35.097 (24.889)	29.784 (9.514)	19.924 (8.289)	30.983 (8.942)	42.771 (11.524)	38.516 (9.000)	51.667 (5.885)
	8	8.107	< 0.001	I-III; I-IV; I-VI; I-VII; I-VIII; I-IX; II-VII; II-IX; IV-VII; IV-IX	19.109 (6.871)	13.784 (7.564)	13.422 (15.535)	4.696 (4.447)	4.023 (4.569)	9.008 (7.299)	8.153 (5.162)	0.000 (0.000)	4.637 (4.072)	0.000 (0.000)
	9	1.548	0.144		4.222 (4.971)	3.389 (5.013)	1.667 (3.750)	1.357 (2.893)	1.667 (3.600)	4.039 (5.441)	1.538 (3.243)	0.714 (2.259)	0.769 (2.433)	0.000 (0.000)
	10	8.596	< 0.001	I-II/III; I-IX; II/III-V; II/III-VI; II/III-VIII; III-I; III-II; III-IV; III-V; III-VI; I-VIII	15.147 (7.317)	11.674 (7.690)	2.011 (3.588)	1.176 (2.480)	13.466 (9.468)	21.308 (11.569)	15.279 (9.650)	6.808 (5.205)	9.973 (5.104)	2.361 (4.988)
	11	2.258	0.025	I-VIII; II-VIII; VIII-IX	5.916 (3.383)	3.893 (4.453)	8.910 (6.894)	6.411 (9.834)	9.634 (11.083)	11.721 (8.464)	11.442 (10.400)	14.009 (11.658)	14.455 (6.388)	3.611 (5.827)

	CFG	F	P	Tukey/ Games Howell	II/III	III	IV	V	VI	VII	VIII	IX
HOLARCTIC ANALYSES	1	2.634	0.021	V-IX	2.778 (3.928)	7.802 (6.954)	7.652 (7.406)	4.995 (5.550)	6.815 (5.821)	6.725 (6.984)	8.333 (3.988)	15.306 (5.564)
	2	2.81	0.015		5.556 (7.857)	3.243 (5.186)	1.250 (3.536)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)
	3	1.089	0.384		0.000 (0.000)	0.000 (0.000)	0.833 (2.357)	3.241 (5.097)	2.738 (4.272)	2.047 (4.100)	3.830 (4.077)	1.000 (3.162)
	4	5.109	< 0.001	III-V; III-VI; III-VII; III-VIII; III-IX	33.333 (15.713)	41.190 (13.055)	30.332 (13.264)	22.837 (5.885)	19.669 (8.641)	23.151 (8.657)	17.078 (5.386)	26.056 (5.054)
	5	2.242	0.046		0.000 (0.000)	2.369 (3.751)	1.795 (3.335)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)
	6	1.655	0.141		0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	2.244 (4.611)	0.000 (0.000)	2.409 (3.923)	0.000 (0.000)
	7	11.235	< 0.001	II/III-IX; III-VII; III-IX; IV-VII; IV-IX; V-VII; V-VIII; V-IX; VI-IX; VIII-IX	25.000 (3.928)	26.689 (7.551)	29.294 (8.302)	19.993 (8.494)	31.251 (9.442)	42.948 (10.889)	38.516 (9.000)	51.667 (5.885)
	8	5.203	< 0.001	VI-VII; VI-IX	5.556 (7.857)	6.715 (4.087)	3.045 (4.300)	6.798 (7.543)	9.059 (4.555)	0.000 (0.000)	4.637 (4.072)	0.000 (0.000)
	9	3.817	0.002		8.333 (3.928)	2.262 (3.551)	2.083 (3.959)	6.731 (5.616)	1.709 (3.392)	0.893 (2.525)	0.769 (2.433)	0.000 (0.000)
	10	6.522	< 0.001	II/III-V; II/III-VI; II/III-VIII; III-V; III-VIII; V-IX	0.000 (0.000)	1.961 (3.038)	13.459 (9.669)	20.870 (9.693)	13.802 (8.956)	6.725 (4.495)	9.973 (5.104)	2.361 (4.988)
	11	2.126	0.057	VIII-IX	19.444 (3.928)	7.768 (12.035)	10.256 (11.880)	14.535 (9.497)	12.713 (10.174)	17.511 (10.230)	14.455 (6.388)	3.611 (5.827)

Supplementary data 4.4. *Continued.*

	CFG	F	P	Tukey/ Games-Howell	I	II	II/III	III
PALAEOTROPIC ANALYSES	1	4.869	0.016	I-II	0.769 (1.720)	10.430 (5.634)	11.380 (7.945)	15.000 (2.357)
	2	0.995	0.424		12.446 (8.448)	8.952 (10.422)	18.651 (19.036)	24.583 (6.482)
	3	3.148	0.059		3.636 (3.358)	0.725 (1.775)	0.000 (0.000)	0.000 (0.000)
	4	1.211	0.342		35.465 (9.471)	34.450 (8.513)	25.925 (15.646)	22.500 (3.536)
	5	3.702	0.038		0.000 (0.000)	1.885 (3.068)	3.845 (2.449)	5.417 (1.768)
	6	.	.		0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)
	7	1.802	0.193	II-III	8.649 (9.683)	17.088 (1.948)	18.844 (11.422)	20.417 (0.589)
	8	0.662	0.589		12.849 (1.754)	9.101 (4.415)	15.178 (19.871)	3.333 (4.714)
	9	4.537	0.02	I-II/III; I-III	8.444 (3.321)	4.606 (5.910)	0.000 (0.000)	0.000 (0.000)
	10	3.277	0.053		13.054 (7.523)	10.679 (9.121)	2.023 (2.995)	0.000 (0.000)
	11	1.448	0.271		4.689 (4.593)	2.086 (2.287)	4.154 (4.210)	8.750 (6.482)

	CFG	F	P	Tukey/ Games-Howell	II/III	III	IV	V	VI	VII	VIII	IX
NEARCTIC ANALYSES	1	4.632	0.004	IV-IX; V-IX; VI-IX; VII-IX	2.778 (3.928)	2.941 (4.159)	0.000 (0.000)	4.167 (5.893)	3.662 (4.468)	1.316 (2.632)	5.994 (3.436)	12.278 (2.609)
	2	7.898	< 0.001	III-IV; III-V; III-VI; III-VII; III-VIII; III-IX	5.556 (7.857)	9.729 (2.880)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)
	3	2.332	0.07		0.000 (0.000)	0.000 (0.000)	3.333 (4.714)	9.722 (1.964)	6.162 (4.533)	4.094 (5.296)	7.660 (0.851)	2.000 (4.472)
	4	1.255	0.326		33.333 (15.713)	27.149 (5.119)	31.667 (2.357)	25.000 (11.785)	24.409 (10.291)	28.841 (7.117)	18.109 (6.625)	28.778 (5.006)
	5	.	.		0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)
	6	0.519	0.808		0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	1.667 (3.727)	0.000 (0.000)
	7	9.734	< 0.001	II/III-IX; III-IX; IV-IX; V-IX; VII-IX; VIII-IX	25.000 (3.928)	20.362 (3.839)	25.000 (7.071)	27.778 (7.857)	30.117 (7.121)	33.371 (4.837)	34.551 (5.744)	50.000 (3.928)
	8	3.74	0.011		5.556 (7.857)	6.787 (1.280)	0.000 (0.000)	0.000 (0.000)	5.585 (3.997)	0.000 (0.000)	6.122 (3.526)	0.000 (0.000)
	9	6.127	0.001		8.333 (3.928)	6.787 (1.280)	8.333 (2.357)	0.000 (0.000)	1.923 (3.846)	1.786 (3.571)	0.000 (0.000)	0.000 (0.000)
	10	0.824	0.58		0.000 (0.000)	2.941 (4.159)	3.333 (4.714)	9.722 (1.964)	6.162 (4.533)	3.816 (4.812)	6.122 (3.526)	4.722 (6.485)
	11	14.923	< 0.001	II/III-IX; III-IX; IV-IX; V-IX; VI-IX; VII-IX; VIII-IX	19.444 (3.928)	23.303 (0.320)	28.333 (2.357)	23.611 (1.964)	21.981 (6.005)	26.777 (3.394)	19.776 (4.129)	2.222 (4.969)

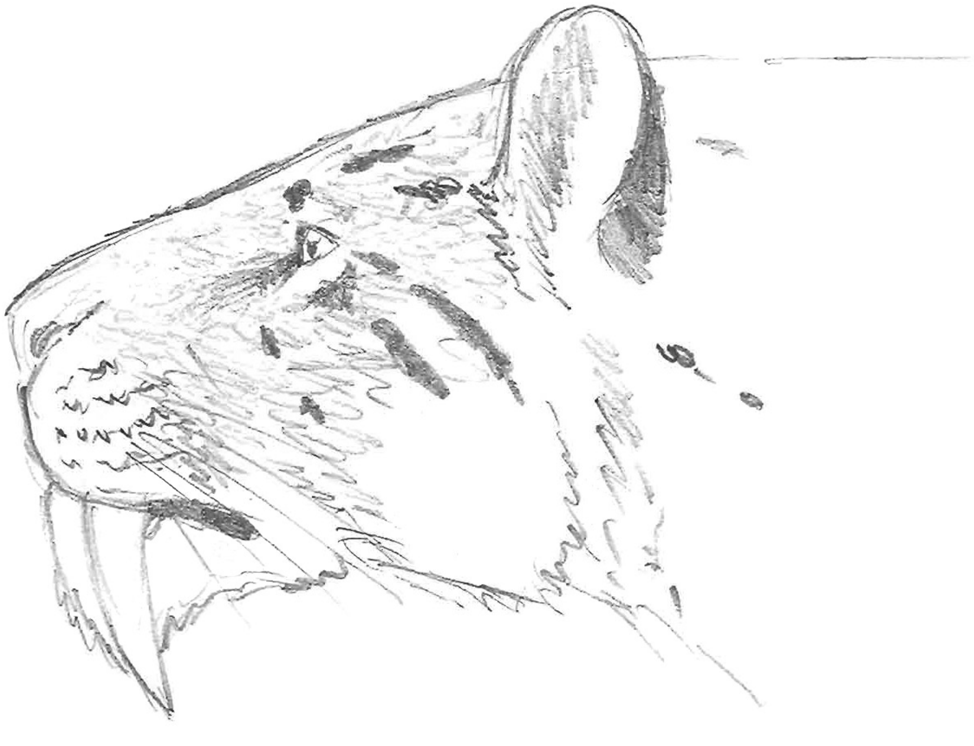
	CFG	F	P	Tukey/ Games-Howell	I	II	II/III	III	V	VII
NEOTROPIC ANALYSES	1	.	.		0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)
	2	1.426	0.279		3.205 (4.395)	3.125 (6.250)	3.704 (6.415)	0.000 (0.000)	3.333 (5.774)	12.698 (2.245)
	3	0.897	0.511		3.938 (3.623)	6.709 (5.862)	2.778 (4.811)	0.000 (0.000)	3.333 (5.774)	0.000 (0.000)
	4	1.353	0.303		15.020 (6.542)	24.183 (5.586)	28.519 (5.702)	25.000 (35.355)	26.190 (5.408)	38.095 (6.734)
	5	.	.		0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)
	6	.	.		0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)
	7	5.445	0.006		28.084 (2.277)	23.841 (6.625)	36.111 (12.729)	75.000 (35.355)	18.095 (10.530)	42.063 (19.081)
	8	7.579	0.002	I-II; I-VII; II-III; II-VII	25.369 (2.276)	20.808 (5.432)	15.741 (13.702)	0.000 (0.000)	14.762 (5.017)	0.000 (0.000)
	9	0.684	0.644		0.000 (0.000)	1.563 (3.125)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)
	10	4.441	0.014	II/III-V; III-V	17.240 (7.274)	13.167 (5.815)	3.333 (5.774)	0.000 (0.000)	27.619 (13.197)	7.143 (10.102)
	11	2.883	0.058		7.144 (0.940)	6.605 (5.867)	9.815 (1.398)	0.000 (0.000)	6.667 (5.774)	0.000 (0.000)

Supplementary data 4.4. *Continued.*

	CFG	F	P	Tukey/ Games-Howell	III	IV	V	VI	VII	VIII	IX
PALAEARCTIC ANALYSES	1	1.964	0.108		10.233 (7.155)	10.203 (6.749)	5.409 (6.251)	9.338 (5.908)	12.134 (5.374)	10.673 (3.207)	18.333 (6.319)
	2	0.709	0.645		0.000 (0.000)	1.667 (4.082)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)
	3	.	.		0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)
	4	7.985	< 0.001	III-IV; III-V; III-VI; III-VII; III-VIII; III-IX	48.211 (8.841)	29.887 (15.629)	21.756 (2.599)	15.876 (5.428)	17.462 (6.155)	16.047 (4.326)	23.333 (3.727)
	5	2.123	0.085		3.554 (4.224)	2.393 (3.722)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)
	6	1.888	0.121		0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	4.038 (5.785)	0.000 (0.000)	3.152 (4.400)	0.000 (0.000)
	7	10.894	< 0.001	III-VII; III-IX; IV-VII; IV-IX; V-VII; V-VIII; V-IX; VI-VII; VI-IX	29.853 (7.077)	30.725 (8.756)	16.100 (6.249)	32.158 (11.745)	52.525 (2.945)	42.480 (10.485)	53.333 (7.454)
	8	5.899	0.001	VI-VII; VI-IX	6.679 (5.224)	4.060 (4.577)	10.197 (6.973)	11.838 (2.792)	0.000 (0.000)	3.152 (4.400)	0.000 (0.000)
	9	12.547	< 0.001	III-V; IV-V; V-VI; V-VII; V-VIII; V-IX	0.000 (0.000)	0.000 (0.000)	10.097 (2.695)	1.538 (3.440)	0.000 (0.000)	1.538 (3.440)	0.000 (0.000)
	10	15.802	< 0.001	III-IV; III-V; III-VI; III-VII; III-VIII	1.471 (2.941)	16.835 (8.470)	26.444 (5.570)	19.915 (6.320)	9.634 (1.198)	13.824 (3.016)	0.000 (0.000)
	11	2.096	0.088	III-VII; III-VIII	0.000 (0.000)	4.231 (4.711)	9.996 (8.164)	5.299 (5.035)	8.245 (1.918)	9.134 (1.999)	5.000 (6.847)

	CFG	F	P	Tukey/ Games-Howell	I	II	II/III	III
AFROTROPIC ANALYSES	1	5.018	0.03	I-II	0.000 (0.000)	15.297 (2.520)	12.558 (8.655)	15.000 (2.357)
	2	0.235	0.869		18.180 (2.162)	17.903 (5.582)	23.314 (18.391)	24.583 (6.482)
	3	14.501	0.001	I-II; I-II/III; I-III	6.060 (0.721)	1.449 (2.510)	0.000 (0.000)	0.000 (0.000)
	4	2.222	0.163		40.197 (3.458)	32.039 (3.572)	22.407 (15.617)	22.500 (3.536)
	5	3.767	0.059		0.000 (0.000)	1.389 (2.406)	3.140 (2.164)	5.417 (1.768)
	6	.	.		0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)
	7	3.358	0.076		1.754 (3.039)	16.686 (0.696)	16.888 (12.184)	20.417 (0.589)
	8	0.477	0.707		12.120 (1.442)	5.560 (2.408)	15.640 (22.914)	3.333 (4.714)
	9	16.973	0.001	I-II/III; I-III	6.060 (0.721)	1.333 (2.309)	0.000 (0.000)	0.000 (0.000)
	10	14.458	0.001	II-III	7.814 (2.358)	4.171 (0.174)	0.862 (1.724)	0.000 (0.000)
	11	0.968	0.454		7.814 (2.358)	4.171 (0.174)	5.192 (4.055)	8.750 (6.482)

		Levene's Test		*t-test*						
	CFG	F	Sig.	t	df	Sig. (2-tailed)	Mean Difference	std. Error Difference	Upper 95% CI	Lower 95% CI
INDOMALAYSIA ANALYSES	1	5,24	0,11	-2,06	3	0,13	-3,64	1,77	-9,26	1,98
	2			1,34	3	0,27	3,85	2,87	-5,28	12,97
	3	-	-	-	-	-	-	-	-	-
	4	0,01	0,93	-0,74	3	0,51	-8,50	11,41	-44,81	27,82
	5	9,60	0,05	-0,77	3	0,50	-2,38	3,07	-12,16	7,40
	6	-	-	-	-	-	-	-	-	-
	7	3,84	0,14	0,69	3	0,54	1,50	2,18	-5,45	8,45
	8	0,27	0,64	0,64	3	0,57	1,30	2,03	-5,16	7,76
	9	4,83	0,12	0,78	3	0,49	4,14	5,28	-12,65	20,93
	10	2,86	0,19	0,54	3	0,63	3,73	6,90	-18,22	25,67
	11	-	-	-	-	-	-	-	-	-



5. LA BREA TAR PITS FUNCTIONAL STRUCTURE OF THE CARNIVORE FAUNA: AN ECOLOGICAL APPROACH TO THE NORTH AMERICAN PLEISTOCENE LANDSCAPE.

Abstract

The study of fossil faunas and its response to past climatic shifts gives relevant information about how changes in the climatic regimens shape the mammalian communities. We used the carnivore mammal associations from La Brea Tar Pits (Los Angeles, CA) found in pits 16+91 and 10+(61/67) to analyse how Late Pleistocene and Holocene climatic changes altered the structure of the mammalian communities from south-western North America over the past 30.000 years. In order to describe the structure of these communities, we applied the Carnivore Functional Groups method (CFG), which allows analysing how the functional spectra of modern Nearctic localities change due to variation in environmental conditions (type of biome). We determined the ecological features of every species in La Brea Tar Pits by means of morphofunctional analyses and, subsequently we assigned every fossil species to a functional group, which allowed defining the functional spectra of La Brea Tar Pits communities. Finally, in order to define its particular climatic regime (type of biome), we compared the Rancho la Brea carnivore communities with the modern ones by means of discriminant analyses. Our analyses successfully detected the climatic shifts associated with Late Pleistocene and Holocene climate changes, inferring a taiga-type boreal forest associated to the post-glacial Holocene association, whereas a sclerophyllous woodland-shrubland is detected for the late Pleistocene carnivore community and in modern Los Angeles. These differences among carnivore communities were due to the greater presence of scansorial predators and relative underrepresentation of ambulatory omnivores during cold and relatively humid conditions, associated to the post-glacial phase. Its absence in the late Pleistocene carnivore association and in the modern community of Los Angeles reflects an increase of the aridity associated to the glacial phase and Holocene warming respectively. Finally, since all extinct giant cursorial hipercarnivores were members of the same functional group, it seems that the Holocene megafaunal extinction in the carnivore guild could be associated to a bottom up process caused by megaprey extinction.

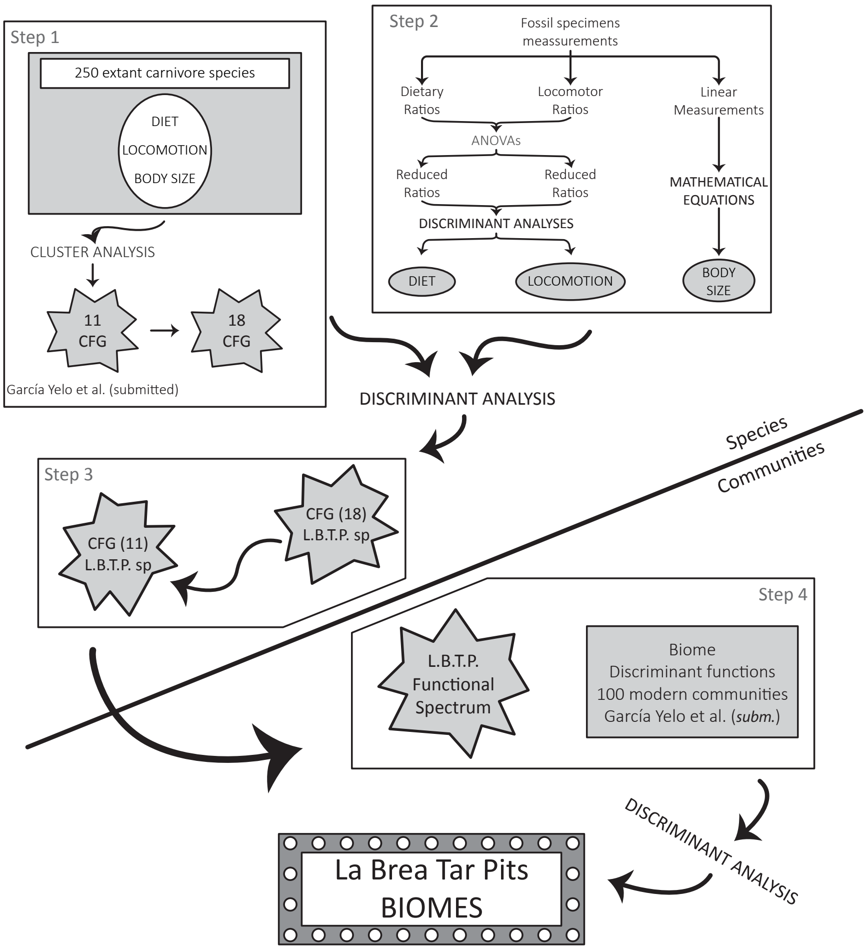
Introduction

Although, human activities are exerting a clear influence, climate change is a natural process (Kalnay & Cai 2003, Canadell et al. 2007, Eyring et al. 2010, IPCC 2013, Liu et al. 2013). The new climatic regimens associated to the induced green house effect influence all ecosystems, forcing species to get adapted to new conditions in a short time (Walther et al. 2002, Parmesan & Yohe 2003, Root et al. 2003, Harley et al. 2006, Cleland et al. 2007, Thuiller 2011, Dullinger et al. 2012). Responses to climatic change in mammal communities have been intensely analysed (e.g. Humphries et al. 2004, Moritz et al. 2008, Lawler et al. 2009, Úbeda et al. 2013). Nevertheless, additionally to the actuo-ecological approach of these studies, the analysis of past mammalian communities and its reaction to climatic changes (Graham et al. 1996, Bobe et al. 2002, deMenocal 2004, Hernández Fernández et al. 2006, Blois et al. 2010, Palombo 2010, Gómez Cano et al. 2013, Rosvold et al. 2013) allow us to better understand the consequences of climate change processes on modern mammal communities. The late Pleistocene and Holocene faunas from la Brea Tar Pits (Los Angeles, California) appear as good proxies to analyse how past climatic conditions shaped the mammal fauna of western North America. Nevertheless, although the carnivore mammals from this fossil site, exceptionally well preserved and diverse (Stock & Harris 2001), have been deeply studied, most of the palaeoecological researches focused its interest in some particular species, analysing how the climatic oscillations affected its ecological traits or its morphology (Binder et al. 2002, Bump et al. 2007, Madan et al. 2011, Hartsone-Rose et al. 2012, Prothero et al. 2012), ecological behavior (Van Valkenburgh & Hertel 1993, McCall et al. 2003, Coltrain et al. 2004, Feranec 2004, Fox-Dobb et al. 2007, Carbone et al. 2009, Kiffner 2009, Van Valkenburgh et al. 2009, O'Keefe et al. 2014), or the existence of sexual dimorphism (Jefferson 1992, Meachen-Samuels & Binder 2009). A palaeosynecological analysis of the community may offer new insights about how climatic oscillations shaped the whole community structure of the carnivore fauna of south-western North America (Meachen-Samuels & Roberts 2014).

The main goal of our research is to analyse how the Pleistocene glacial climate and the Holocene warming affected the carnivore mammal community from south-western North America during the last 30,000 years, comparing the carnivore mammal community structure from La Brea Tar Pits with the extant community present in Los Angeles (California, USA) today.

Material and Methods

Figure 5.1. *Flux diagram explaining the analytical process followed in this research. CFG, Carnivore functional groups; LBTP, La Brea Tar Pits.*



A flux diagram explaining the analytical process followed in this research is included (fig. 5.1) in order to explain the different steps followed to infer the ecological behaviour of the carnivore species from La Brea Tar Pits, and to analyse the climatic changes suffered in south-western North America during last 30,000 years.

Carnivore assemblages from La Brea Tar Pits

All data from La Brea Tar Pits fossil site were collected from the carnivore mammals collection housed in the Page Museum at La Brea Tar Pits, Los Angeles (CA, USA). Over 1200 skeletal remains were measured by one of the authors (BAGY), in order to collect the information needed to infer the ecological behaviour (locomotion and diet) and the mean body size of the carnivore mammal species conforming the carnivore communities from La Brea Tar Pits (supplementary data 5.1). As long as possible, we measured 10 elements of every taxon. Due to the size and shape stasis

		B S (g) - modern	B S (g) - inferred	B S Category	Feeding Habits	Locomotor Behaviour	Inferred CFG	Pit 91	Pit 61/67	Los Angeles
Canidae	*Canis lupus*	39875.0	39830.6	Large	Hipercarn. (Carn.)*	Curs.	1	x	x	
Canidae	Canis dirus†	-	60828.7	Mega	Hipercarn.	Curs.	1	x	x	
Felidae	*Panthera atrox*†	-	224584.4	Mega	Hipercarn.	Curs.	1	x	x	
Felidae	*Smilodon fatalis*†	-	200552.8	Mega	Hipercarn.	Curs.	1	x	x	
Canidae	*Urocyon cinereoargenteus*	3833.7	4435.6	Small (Medium)*	Carn.	*Amb.*	4	x	x	x
Mustelidae	*Taxidea taxus*	7107.6	6308.8	Medium	Carn.	Fss.	4	x	x	x
Canidae	*Canis latrans*	13406.3	18899.4	Medium (Large)*	Carn.	Amb. (Curs.)*	4 (1)	x	x	x
Felidae	*Lynx rufus*	8904.1	12272.2	Medium	Hipercarn.	*Amb.*	7	x	x	x
Felidae	*Puma concolor*	51600.0	53329.2	Mega	Hipercarn.	Amb.	7	x	x	x
Felidae	*Panthera onca*	100000.0	88960.5	Mega	Hipercarn.	*Amb.*	7		x	
Mustelidae	*Mustela frenata*	147.0	210.3	Micro	Hipercarn.	*Amb.*	7	x	x	x
Felidae	*Leopardus cf. wiedii*	3250	3067.7	Small	*Hipercarn.*	*Sc.*	8		x	
Procyonidae	*Bassariscus astutus*	1129.5	*1129.5*	*Small*	*Omn.*	*Sc.*	9	x	x	x
Mephitidae	*Spilogale putorius*	341.0	476.9	Micro	*Omn.*	*Amb.*	11	x	x	x
Mephitidae	*Mephitis mephitis*	2085.0	1359.7	Small	Omn.	*Amb.*	11	x	x	x
Procyonidae	*Procyon lotor*	5525.0	*5525.0*	*Medium*	*Omn.*	*Amb.*	*11*	x		x
Ursidae	*Ursus americanus*	99949.4	91473.7	Mega	Omn.	*Amb.*	11	x	x	
Ursidae	*Arctodus simus*†	-	369244	Mega	Omn.	*Amb.*	11	x		
Ursidae	*Ursus arctos*	172720.4	211463.9	Mega	*Omn.*	Amb.	11		x	x
			Number of species (S)					16	17	11

Table 5.1. *Locomotor and feeding behaviour, and mean body size of the carnivore mammals found La Brea Tar Pits and Los Angeles, together with its inferred carnivore functional group. *, Denotes the corrected ecological features of those species with a high degree of phylogenetic relationship or misclassified due to the intraspecific variability in body size. †, Indicates the extinct species. Values between brackets represent the uncorrected ecological features of the species, together with the inferred functional groups obtained with the uncorrected ecological features. The cursive in the ecological behaviour (or the functional group) of any ancient species denotes that these particular features are those of its living relatives. Ecological categories: Hipercarn., hipercarnivores; Carn., carnivores; Omn., omnivores; Curs., cursorial predators; Amb., ambulatory predators; Fss., fossorial predators; Sc., scansorial predators (table 5.2). Carnivore functional groups as in table 5.3*

in La Brea Tar Pits mammal species (Madan *et al.* 2011, Prothero *et al.* 2012), we only considered differences in species composition of the different pits (communities), and not in the ecology of the same species recorded in different pits. Although size and shape changes in ***Canis dirus*** specimens from different pits has been recently detected (O'Keefe *et al.* 2014), these differences are negligible in our research, as our body size categories for large species include a wide range of body sizes.

Due to the late Pleistocene and Holocene environmental shifts, we analysed how the community structure of the carnivore associations from La Brea Tar Pits changed after the Last Glacial Maximum and the Holocene warming. We focused our interest on four particular pits covering two temporal moments. The carnivore associations from Pit 16 and Pit 91, dated around 26,000 ky and 29,000 ky respectively (Friscia *et al.* 2008, O'Keefe *et al.* 2009), were considered together to analyse the glacial situation, whereas the association of the carnivore communities from Pit 61/67 and Pit 10, dated as 11,500 and 10,000 ky old respectively (Howard 1960, O'Keefe *et al.* 2009), were used to describe the post-glacial conditions (table 5.1). Finally, both associations were compared with the modern carnivore community from in Los Angeles (California), in order to analyse the effects of the Holocene warming.

Carnivore functional groups (step 1 in the diagram flux)

Recently developed by García Yelo *et al.* (*submitted*), the Carnivore Functional Groups new methodology allows gathering the different terrestrial species within the order Carnivora in ecological groups (following Wilson & Reeder 2005). The proportions of these groups describe the ecological structure of the communities and relate its community structure with the climatic characteristics of the environment. These groups were defined by means of cluster analysis, grouping all the extant carnivore species according to their ecological characteristics (diet, locomotion and body size – table 5.2, supplementary data 5.2).

García Yelo *et al.* (*submitted*) found that eleven groups (fig. 5.2, table 5.3) was the optimum number of functional groups to infer the climate. Nevertheless, the capacity of the three ecological variables to assign the extinct species to a particular functional group, only considering 11 CFGs is relatively low (supplementary data 5.2). During the clustering process the different species are assorted in small groups (subgroups) with a higher similarity degree. These groups are also gathered in larger assemblages with lower ecological similarity. Therefore, the different subgroups will be included in a particular CFG, and every species belonging to an specific subgroup will be also related to a particular group. Therefore, we can divide the 11 functional groups in 18 functional subgroups, increasing the similarity degree of the species belonging to these subgroups and, consequently, increasing the predictive power

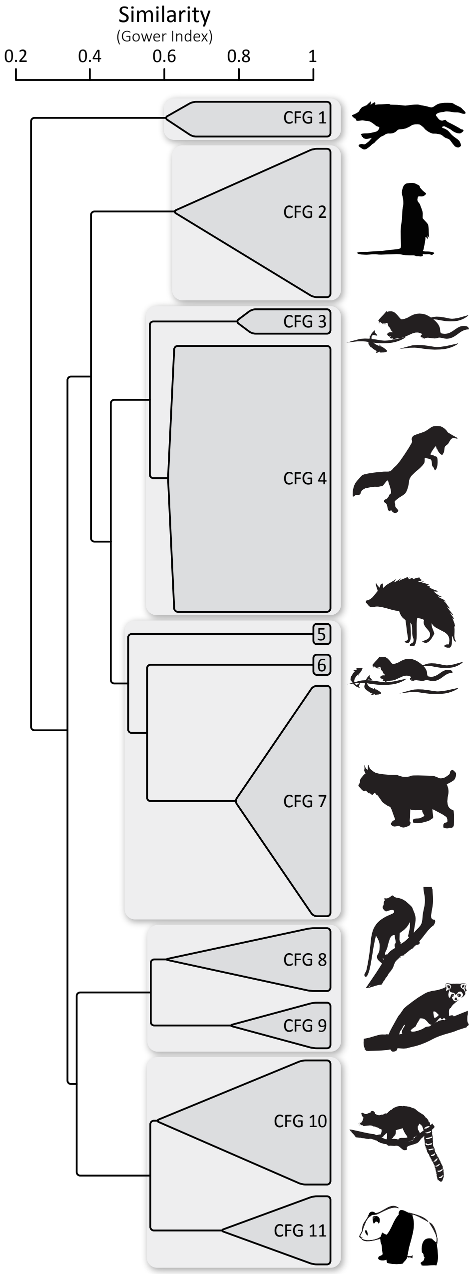


Figure 5.2. *Cluster showing the 11 carnivore functional groups obtained by García Yelo et al. (submitted), based on the ecology of the 250 modern terrestrial carnivore species (table 5.2, supplementary data 5.2).*

of the discrimant function analyses. As a result, we will be able to assign every species from La Brea Tar Pits to a particular functional group with a higher level of confidence (supplementary data 5.2). Once every species from La Brea Tar Pits is assigned to a subgroup it can also be attributed to one of the original 11 CFGs.

Ecological behaviour of La Brea Tar Pits carnivore mammals (step 2 in the flux diagram)

Previously to use the carnivore functional groups methodology, we have to define the ecology of the fauna from La Brea Tar Pits. So to do it, and using different methodological approaches based on biometric ratios previously developed by several authors (supplementary figures 5.1 and 5.2, supplementary data 5.3 and 5.4), we inferred the feeding habits (Van Valkenburgh 1988, 1989, Friscia *et al.* 2006) and the hunting locomotor behaviour (Van Valkenburgh 1985, 1987, Taylor 1989) of the carnivore species from the fossil sites (table 5.1).

We merged Van Valkenburgh (1985, 1987) and Taylor (1989) classifications, dividing Van Valkenburgh's terrestrial locomotion in two categories (cursorial and ambulatory carnivores) and Taylor's arboreal classification in arboreal and scansorial predators (table 5.2). On the other hand, in order to make a single classification including all terrestrial carnivores, we combined Friscia *et al.* (2006) and Van Valkenburgh (1988, 1989) classifications in a single one, separating large omnivores and insectivores and small carnivores e hipercarnivores (table 5.2). Due to the differences between previous locomotor and diet classifications and our ones, we tested whether all biometric ratios included in our analyses

	Taylor 1989	Van Valkenburgh 1985, 1987	García Yelo et al. (submitted)	Description
Locomotion	Cursorial	Terrestrial	Cursorial	Carnivore species, which rarely or never climb, developing a long distance chase and rarely preceded by a stalk.
	Ambulatory		Ambulatory	Carnivore species, which rarely or never climb, developing a short distance search (without chase), ending in either a pounce or a short chase sometimes preceded by a stalk.
	Arboreal	Scansorial		Carnivore species capable of climbing, which usually climbs for escape.
		Arboreall		Carnivore species, which are rarely on the ground, living, foraging and taking shelters in trees.
	Fossorial			Carnivore species digging regularly for both food and shelter.
	Aquatic	-	Aquatic	Carnivore species living and hunting in the water.
Diet	**Friscia et al. 2006**	**Van Valkenburgh 1988, 1989**	**García Yelo et al. (submitted)**	**Description**
	Carnivores	Meat	Hipercarnivores	Carnivore species with more than 70 % of meat included in their diet.
		Meat / Non vertebrate	Carnivores	Carnivore species with 50-69.99 % of meat included in their diet.
	-	Meat / Bone		Carnivore species, which include more than 70 % of meat in their diet, with the addition of large bones.
	Insectivores	Non Vertebrate / Meat	Insectivores	Carnivore species including less than a 50 % of meat in their diet, with a dominion of invertebrates (mainly insects and chelicerates).
	Omnivores		Omnivores	Carnivore species including less than a 50 % of meat in their diet, with a large component vegetable matter and/or hard objects (mollusks or large crustaceans), as well as true omnivores for which no dominant food type could be discerned or species that mainly feed in vegetable matter.
Body Size	Mega-predators			Carnivore species larger than 45 kg.
	Large predators			Carnivore species with a body size ranging between 15 to 44.9 Kg
	Medium predators			Carnivore species with a body size ranging between 4 to 14.9 Kg
	Small predators			Carnivore species with a body size ranging between 1 to 3.9 Kg
	Micro-predators			Carnivore species smaller than 1 kg.

Table 5.2. *Classification of the ecological features used to define the carnivore functional groups, together with the relationship between our classification and the original ones (Van Valkenburgh 1985, 1987, 1988, 1989, Taylor 1989, Friscia et al. 2006).*

(supplementary figures 5.1 and 5.2, supplementary data 5.3 and 5.4) were able to discriminate our locomotor and dietary classifications. We conducted one-way ANOVA analyses on the locomotor and dietary ratios. In addition, a discriminant analysis to infer the carnivore ecological behaviour was performed on a reduced dataset consisting of only those ratios found to differentiate significantly the locomotor and dietary groups according to the previous univariate analyses of variance (ANOVA). Although it is expected that most of the species with modern relatives share their ecological behaviour and body size category, in those few cases where modern and inferred ecology differ, we included both possibilities in our analyses. Finally, for those species without value in some ANOVA ratios, but with modern representatives of the species, we took in consideration the locomotion and diet of the modern representatives of the species.

CFG	Description
1	Medium to mega cursorial hipercarnivores.
2	Ambulatory or fossorial insectivores (< 4 kg.)
3	Aquatic carnivores.
4	Non-aquatic carnivores (mainly arboreal, scansorial and ambulatory predators)
5	Large ambulatory meat/bone eaters (Hyaena hyaena, H. brunnea)
6	Aquatic hipercarnivores.
7	Ambulatory hipercarnivores.
8	Scansorial hipercarnivores (including the insectivorous coatis)
9	Scansorial omnivores
10	Aquatic, arboreal and fossorial omnivores
11	Ambulatory omnivores

Table 5.3. *Description of the 11 Carnivore Functional Groups defined in García Yelo et al. (submitted) and used in our research.*

In the case of the short-faced bear *Arctodus simus*, a species without modern representatives and useful skeletal remains in the fossil site to infer its locomotion, we followed previous studies that classified ***Arctodus simus*** as a large ambulatory omnivore (Emslie & Czaplewski 1985, Matheus 1995, Sorkin 2006, Figueirido *et al*. 2009, 2010). Finally, the locomotor and dietary behaviours of the fossil species were calculated by means of discriminant function analyses (DFA).

In order to infer the mean body size of species from La Brea Tar Pits (table 5.1), we applied the algorithms developed by Van Valkenburgh (1990) for felids, Figueirido *et al*. (2010) for ursids, and Egi (2001) for the rest of the families. While Figueirido *et al*. (2010) and Egi (2001) developed their formulas from linear measurements of several postcranial bones (supplementary figure 5.3, supplementary data 5.5 to 5.7), Van Valkenburgh (1990) found a close relationship between M_1 length and body size in felids. Finally, the arithmetic mean body size of every species was obtained.

Community structure and climate and evolution during last 30,000 years in south-western California (steps 3 and 4 of the flux diagram)

Once the ecological hunting behaviour and mean body size of La Brea Tar Pits species were defined, we were able to obtain the functional spectrum of their communities. Using the ecological characteristics previously established for the La Brea Tar Pits carnivore species, and by means of discriminant analysis, we assigned to a particular functional subgroup, and consequently to a major group, every carnivore species from the fossil site (table 5.1). Following García Yelo *et al.* (*submitted*), we defined the functional spectrum of La Brea Tar Pits as the percentage of species included in each one of the eleven groups.

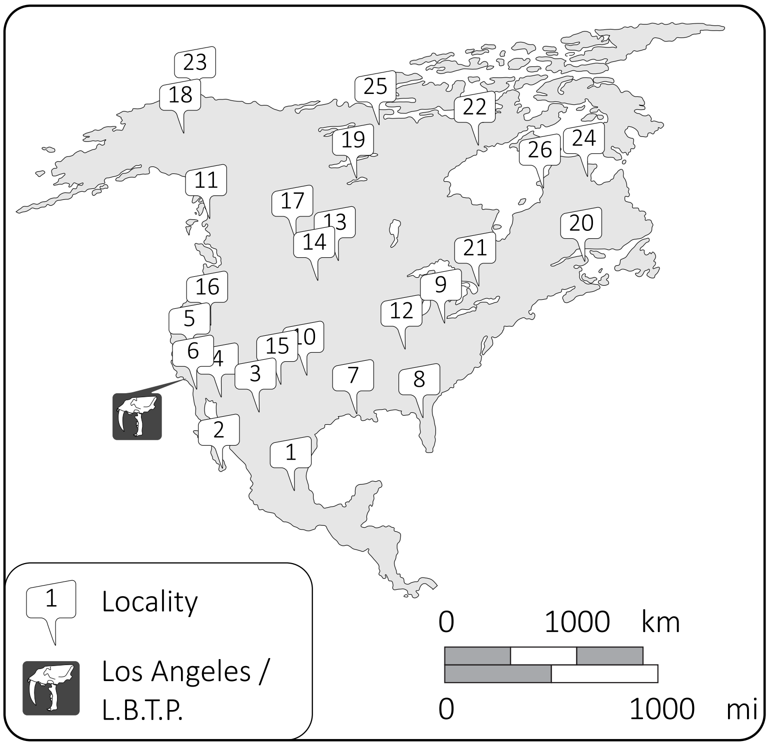


Figure 5.3. *Distribution of the 26 modern localities from the Nearctic studied in this research, together with the geographic situation of La Brea Tar Pits fossil site and Los Angeles extant locality. Extant locality numbers as in supplementary data 5.8 and appendix 1.*

Finally, we used the discriminant functions obtained by García Yelo *et al.* (*submitted*) from 26 modern carnivore communities from North America (fig. 5.3, appendix 1 and supplementary data 5.8) to establish the type of biome (following Walter 1970 and Hernández Fernández 2001) associated to La Brea Tar Pits communities, as well as to the modern Los Angeles fauna.

All statistical analyses were performed in SPSS Statistics v.20 for MacOS X.

Results

Morphofunctional analyses and ecological behaviour on carnivore mammals from La Brea Tar Pits

Tables 5.4 to 5.6 include the results of the ANOVA analyses performed here to identify which ratios help us to discriminate the locomotor or dietary behaviour in the carnivore species.

Tables 5.7 to 5.9 resume the mean values of the ecomorphological ratios used to infer the dietary and locomotor behaviours of the fossil species, together with the predictive power of the equations derived form the discriminant analyses used to infer these ecological features. The predictive power of the discriminant models applied vary between the 66% to 86.5%. When applying these models to the inference of La Brea Tar Pits carnivores, most of the species with modern representatives share

		F	P	Tukey	Arboreal	Scansorial	Cursorial	Fossorial	Ambulatory
Locomotor behaviour	FMT	5.740	0.001	C-Fs; A-Sc; A-Fs	3.743 (0.448)	3.364 (1.011)	2.436 (0.148)	3.856 (1.153)	2.659 (0.626)
	MCP	9.587	< 0.001	C-Arb; C-Sc; C-Fs; A-Arb; A-Sc	1.390 (0.027)	1.697 (0.223)	2.625 (0.364)	1.805 (0.324)	2.255 (0.503)
	OLL	3.417	0.014	A-Fs; Fs-Sc	0.195 (0.007)	0.218 (0.037)	0.231 (0.043)	0.277 (0.041)	0.209 (0.046)
	OLA	4.682	0.003	C-Arb; C-Sc	11.000 (2.828)	15.667 (10.321)	33.200 (4.060)	18.667 (11.587)	22.250 (8.826)
	UD	4.167	0.005	A-Fs; Fs-Sc	2.095 (0.431)	1.661 (0.358)	1.860 (0.395)	2.503 (0.482)	1.925 (0.488)
	ASD	2.997	0.028		0.130 (0.042)	0.166 (0.039)	0.230 (0.061)	0.150 (0.036)	0.192 (0.059)
	ARCH	1.023	0.403		0.217 (0.026)	0.193 (0.035)	0.175 (0.045)	0.151 (0.036)	0.181 (0.058)

Table 5.4. *Results for the ANOVA analyses on ratios to infer the locomotion of the predators from La Brea Tar Pits. Column 'F' lists the F-statistics for univariate analyses of variance (ANOVA) for that particular ratio between the different locomotor groups. 'P' is the P-value for each comparison across all groups. Under each locomotion type is listed the mean and standard deviation, in parentheses, for each ratio. 'Tukey' lists significant differences between: cursorial and arboreal predators (C-Arb), cursorial and scansorial predators (C-Sc), cursorial and fossorial predators (C-Fs), ambulatory and arboreal predators (A-Arb), ambulatory and scansorial predators (A-Sc), ambulatory and fossorial predators (A-Fs), and fossorial and scansorial predators (Fs-Sc) for locomotor behaviour.*

		F	P	Tukey	Hiper-carnivore	Carnivore	Omnivore	Insectivore
Feeding Habits	RLGA	18.375	< 0.001	C-O; C-I; H-O; H-I	0.681 (0.190)	0.850 (0.172)	1.244 (0.408)	1.323 (0.358)
	RUGA	7.988	< 0.001	C-O; C-I; H-O; H-I	0.717 (0.246)	0.840 (0.221)	1.068 (0.296)	1.038 (0.147)
	M1BS	6.557	0.001	H-C; H-O; H-I	0.115 (0.023)	0.093 (0.016)	0.087 (0.032)	0.078 (0.022)
	M2S	14.003	< 0.001	C-O; C-I; H-O; H-I	0.044 (0.016)	0.055 (0.014)	0.069 (0.018)	0.074 (0.009)
	MAT	4.559	0.006	H-C; H-I	0.329 (0.078)	0.274 (0.055)	0.312 (0.066)	0.261 (0.041)
	P4P	17.201	< 0.001	C-O; C-I; H-O; H-I	0.538 (0.060)	0.611 (0.104)	0.833 (0.184)	0.829 (0.199)
	UM21	2.861	0.043	H-I	0.252 (0.352)	0.349 (0.280)	0.353 (0.283)	0.533 (0.190)
	P4S	5.128	0.003	C-O	0.490 (0.084)	0.462 (0.101)	0.587 (0.127)	0.535 (0.113)
	RBL	2.303	0.084		0.667 (0.079)	0.652 (0.058)	0.596 (0.083)	0.622 (0.113)
	IXP4	2.460	0.070		0.061 (0.015)	0.054 (0.013)	0.063 (0.012)	0.056 (0.008)
	IXM2	2.240	0.091		0.066 (0.013)	0.061 (0.014)	0.070 (0.011)	0.062 (0.008)
	MAM	2.318	0.083		0.176 (0.022)	0.170 (0.018)	0.198 (0.078)	0.165 (0.020)
	C1	0.981	0.407		0.711 (0.183)	0.637 (0.141)	0.686 (0.186)	0.633 (0.109)
	PMZ	1.445	0.237		0.219 (0.051)	0.235 (0.062)	0.229 (0.043)	0.258 (0.046)
	P4Z	0.925	0.434		0.099 (0.011)	0.101 (0.014)	0.097 (0.016)	0.105 (0.015)

Table 5.5. *Results for the ANOVA analyses on ratios to infer the feeding habits for small predators. Column 'F' lists the F-statistics for univariate analyses of variance (ANOVA) for that particular ratio between the different dietary groups. 'P' is the P-value for each comparison across all groups. Under each dietary type is listed the mean and standard deviation, in parentheses, for each ratio. 'Tukey' lists significant differences between: carnivores and insectivores (C-I), carnivores and omnivores (C-O), hipercarnivores and insectivores (H-I), hipercarnivores and omnivores (H-O) and hipercarnivores and carnivores (H-C).*

		F	P	Tukey	Hiper-carnivore	Meat-Bone	Carnivore	Omnivore	Insectivore
Feeding Habits	RBL	17.829	< 0.001	H-C, H-O, H-I, M/B-O	0.881 (0.165)	0.855 (0.092)	0.631 (0.054)	0.516 (0.074)	0.603 (0.090)
	RLGA	27.971	0.001	H-C, H-O, H-I, M/B-O, M/B-I, C-O, C-I	0.291 (0.462)	0.210 (0.127)	0.837 (0.189)	1.774 (0.430)	1.518 (0.248)
	RPS	15.307	0.001	C-O, H-O, I-O, M/B-H, M/B-C, M/B-I, M/B-O	2.116 (0.331)	3.570 (0.042)	2.338 (0.213)	1.530 (0.531)	2.362 (0.473)
	PMD	9.982	0.001	C-O, H-O, H-I, M/B-H, M/B-C	0.486 (0.040)	0.630 (0.071)	0.507 (0.074)	0.603 (0.061)	0.589 (0.054)
	CS	0.918	0.461		72.513 (7.383)	71.150 (0.495)	67.893 (7.992)	68.457 (7.200)	71.026 (10.809)

Table 5.6. *Results for the ANOVA analyses on ratios to infer the feeding habits for large predators. Column 'F' lists the F-statistics for univariate analyses of variance (ANOVA) for that particular ratio between the different dietary groups. 'P' is the P-value for each comparison across all groups. Under each dietary type is listed the mean and standard deviation, in parentheses, for each ratio. 'Tukey' lists significant differences between: carnivores and insectivores (C-I), carnivores and omnivores (C-O), hipercarnivores and insectivores (H-I), hipercarnivores and omnivores (H-O), hipercarnivores and carnivores (H-C), meat/bone eaters and insectivores (M/B-I), meat/bone eaters and omnivores (M/B-O), meat/bone eaters and carnivores (M/B-C), meat/bone eaters and hipercarnivores (M/B-H) and insectivores and omnivores (I-O).*

the same ecological behaviour with its modern relatives. Nevertheless, some species are classified by the discriminant analyses in a different ecological category. These species are the grey wolf (*Canis lupus*), misclassified as carnivorous species instead of hipercarnivorous one, and the coyote (*Canis latrans*), defined as a cursorial predator instead of ambulatory one. The coyote, a middle-sized carnivore, is also assigned to the group of large predators. Finally, the ancient representative of the grey fox (*Urocyon cinereoargenteus*), slightly heavier than its modern relative, is included in the medium size category. The mean body sizes of both species are close to the small to medium and medium to large body size boundaries. Consequently, a slight difference in their inferred body sizes, due to intraspecific variability in animal's body size, causes a wrong assignation in body size category.

Table 5.1 exposes the carnivore functional group assigned to each species by the second discriminant model applied in our research. The high predictive power of this discriminant analysis, with the 99.2% of the extant species correctly classified (supplementary data 5.2), allows us to assume that the assigned functional group for the extinct species actually represents its true ecological category. In the case of the ecological assignment of the three ambiguously classified species, whereas the coyote is included in a different group when the corrected and uncorrected ecological features are considered, we detected no effect on the functional group designation for the grey wolf and the grey fox cases (table 5.1).

	Feeding habits ratios														
	RLGA*	RUGA*	M1BS*	M2S*	MAT*	P4P*	UM21*	P4S*	RBL	IXP4	IXM2	MAM	C1	PMZ	P4Z
Bassariscus astutus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Procyon lotor	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mustela frenata	0.473	0.574	0.154	0.041	0.384	0.511	0	0.594	0.699	0.072	0.071	0.183	-	0.291	0.115
Spilogale putorius	-	0.984	0.121	-	0.354	0.631	0	0.719	0.593	0.071	0.073	0.213	0.586	0.247	0.126
Mephitis mephitis	1.024	1.086	0.126	0.083	0.325	0.734	0	0.668	0.577	0.063	0.071	0.218	0.566	0.228	0.102
Leopardus cf. wiedii	0	0	-	-	0.275	-	0	-	1	0.067	0.065	0.204	-	-	-
Urocyon cinereoargenteus	0.827	0.984	0.094	-	0.230	0.466	0.679	0.442	0.643	0.051	0.056	0.189	0.525	0.216	0.084
Correctly classified extant species (%)								73							

Table 5.7. *Mean values of the ecomorphological ratios used to infer the diet of the fossil species found in La Brea Tar Pits (for small predators). *, Denotes those ratios showing a discriminant capacity in the ANOVA results to discriminate the diet of the carnivore species (table 5.5). Additionally, the predictive power of the equations derived form the discriminant analyses used to infer these ecological features is included at the end of the table.*

	Feeding habits ratios				
	RBL*	RLGA*	RPS*	PMD*	CS
Taxidea taxus	0.651	0.845	2.548	0.544	77.1
Lynx rufus	1	0	2.037	0.486	86.4
Canis latrans	0.702	0.714	2.136	0.432	63.5
Canis lupus	0.712	0.748	2.422	0.503	68.0
Puma concolor	1	0	2.445	0.542	84.5
Canis dirus†	0.747	0.659	1.019	0.533	71.9
Panthera onca	1	0	2.202	0.492	81.9
Ursus americanus	0.612	1.983	1.387	0.638	67.5
Ursus arctos	0.605	1.982	-	-	-
Smilodon fatalis†	1	0	1.999	0.444	51.5
Panthera atrox†	1	0	2.333	0.487	73.6
Arctodus simus†	0.685	1.677	1.019	0.565	47.0
Correctly classified extant species (%)			86.5		

Table 5.8. *Mean values of the ecomorphological ratios used to infer the diet of the fossil species found in La Brea Tar Pits (for large predators). *, Denotes those ratios showing a discriminant capacity in the ANOVA results to discriminate the diet of the carnivore species (table 5.6). Additionally, the predictive power of the equations derived from the discriminant analyses used to infer these ecological features is included at the end of the table.*

	Locomotor behaviour ratios						
	FMT*	MCP*	OLL*	OLA*	ASD*	UD*	ARCH
Bassariscus astutus	-	-	-	-	-	-	-
Procyon lotor	-	-	-	-	-	-	-
Mustela frenata	-	-	0.187	4.903	-	-	-
Spilogale putorius	-	-	0.209	7.406	-	-	-
Mephitis mephitis	2.762	-	0.206	10.840	0.067	2.042	0.108
Leopardus cf. wiedii	-	-	0.160	3.108	-	-	-
Urocyon cinereoargenteus	2.211	2.260	-	-	0.258	1.851	0.172
Taxidea taxus	3.383	1.523	0.331	14.245	0.078	2.207	0.136
Lynx rufus	2.299	2.166	-	-	0.163	1.075	0.203
Canis latrans	2.224	2.701	0.201	32.947	0.242	1.971	0.140
Canis lupus	2.304	2.306	0.217	27.915	0.233	1.622	0.182
Puma concolor	2.760	2.084	0.229	19.874	0.189	1.305	0.235
Canis dirus†	2.438	2.582	0.256	36.244	0.243	2.116	0.184
Panthera onca	-	-	-	-	0.165	-	-
Ursus americanus	-	-	-	-	-	1.033	0.271
Ursus arctos	4.716	2.299	0,238	17.691	0.124	2.034	0.120
Smilodon fatalis†	3.666	1.883	0.307	34.212	0.125	1.149	0.235
Panthera atrox†	2.802	1.971	0.284	36.822	0.159	1.185	0.242
Arctodus simus†	3.993	2.182	-	-	0.122	1.799	0.179
Correctly classified extant species (%)				66			

Table 5.9. *Mean values of the ecomorphological ratios used to infer the locomotion of the fossil species found in La Brea Tar Pits. *, Denotes those ratios showing a discriminant capacity in the ANOVA results to discriminate the locomotor behaviour of the carnivore species (table 5.4). Additionally, the predictive power of the equations derived form the discriminant analyses used to infer these ecological features is included at the end of the table.*

Locality	S	CI	GFC										
			1	2	3	4	5	6	7	8	9	10	11
Los Angeles	11	IV	0	0	0	27.27	0	0	27.27	0	9.1	0	36.36
Pit 61/67 (correct.)	17	VIII	23.53	0	0	17.65	0	0	23.53	5.88	5.88	0	23.53
Pit 61/67	17	VIII	29.41	0	0	11.77	0	0	23.53	5.88	5.88	0	23.53
Pit 91 (correc.)	16	IV	25	0	0	18.75	0	0	18.75	0	6.25	0	31.25
Pit 91	16	IV	31.25	0	0	12.5	0	0	18.75	0	6.25	0	31.25

Table 5.10. *Carnivore functional spectra of La Brea Tar Pits and Los Angeles carnivore for the corrected and uncorrected versions. CI, Inferred biome: IV, sclerophyllous woodland-shrubland; VIII, Taiga forest. S, species number.*

Carnivore functional structure and biome inference for the carnivore communities from La Brea Tar Pits

Table 5.10 exposes the functional spectra of the different communities found in south-western North America during late Pleistocene and Holocene, together with the one found in Los Angeles today. We included the corrected and uncorrected functional group assignation of the coyote in our analyses to compare the results.

While five functional groups are not represented in any temporal stage of the carnivore communities from south-western North America (CFG 2, CFG 3, CFG 5, CFG 6 and CFG 10), four of them are represented in all of them (CFG 4, CFG 7, CFG 9 and CFG 11). Finally, while CFG 1 is just represented in the late Pleistocene and early Holocene communities, CFG 8 is exclusive of the Holocene community (table 5.10).

Supplementary data 5.8 exposes the carnivore functional spectra of the 26 Nearctic localities included in García Yelo *et al.* (*submitted*) to obtain the discriminant functions used to infer the type of biome. With a high discriminant capacity (80,8% of correctly classified localities), we were able to apply these discriminant functions to our ancient communities. When applying the discriminant functions developed in García Yelo *et al.* (*submitted*), we found no difference between the corrected and uncorrected version, giving the same results. This model identified the sclerophyllous woodland-shrubland biome found in south-western California today, and shows how the environment changed during last 30,000 years. While a sclerophyllous woodland-shrubland (biome IV) is inferred for the late Pleistocene association, a taiga forest (biome VIII) is detected for the early Holocene one, reflecting a change to more forested and humid conditions between the late Pleistocene and the early Holocene in south-western California.

Discussion

Ecology of the carnivore fauna from La Brea Tar Pits

The ecological behaviour of the Pleistocene carnivore faunas found in La Brea Tar Pits is highly similar to the one found in Los Angeles, with most of the species sharing the same hunting behaviour with its relatives today (table 5.1, supplementary data 5.2). Nevertheless a structural change is observed, as some species, mainly affected by the Pleistocene megafauna turnover, have no representatives in the order Carnivora today. These species are two large felids (*Smilodon fatalis* and *Panthera atrox*), the dire wolf (*Canis dirus*) and the 'short-faced' bear (*Arctodus simus*). In our results, we confirm the hypotheses previously established for these species' ecology. All felids, together with the canid, are large cursorial predators (***e.g.*** Anyonge 1993, 1996, Van Valkenburgh & Hertel 1993, Anyonge *et al.* 2003, Coltrain *et al.* 2004, Christiansen & Harris 2005, Anyonge & Baker 2006, Van Valkenburgh 2007, Koper & Naples 2011, Rizk *et al.* 2012) highly specialized in hunting large herbivores, and all belonging to CFG 1. The inferred ecology for the ursid *Arctodus simus*, a large omnivore (CFG 11), also agrees with previous researches (Emslie & Czaplewski 1985, Matheus 1995, Sorkin 2006, Figueirido *et al.* 2009, 2010).

On the other hand, some fossil species with extant relatives might have a different ecology. The different classification of the grey wolf and the coyote seems to reflect the high influence of the phylogenetic constrains in the morphology of the canids. Both species are phylogenetically close (Zrzavy & Ricankova 2004, Lindblad-Toh *et al.* 2005, Nyakatura & Bininda-Emonds 2012), with similar adaptations to pursuit during hunting (elongated for and hind limbs) and with their dentaries adapted to an opportunistic diet where meat is the main, but not the only available food. Consequently, these species are both classified as cursorial carnivores, despite the hipercarnivorous wolf includes a higher percentage of meat than the coyote in its diet, and the ambulatory coyote does not normally develop the pursuit during hunting.

Climate and community structure evolution during last 30,000 years in south-western California

Variations in the structure of the carnivore mammal associations from La Brea Tar Pits (Los Angeles, California) reflect a change from semiarid sclerophyllous woodland-shrubland during the glacial phase to a postglacial humid taiga forest. Finally, the structure of carnivore community of Los Angeles reflected an increase in the aridity associated to the Holocene warming, detecting the sclerophyllous woodland-shrubland found in the area today.

The biogeographic location of La Brea Tar Pits, in the southern limits of the cold and temperate Pleistocene forests, allowed surviving a variety of species from different environmental landscapes, due to the mixture between oak woodland, chaparral and pine forests (Coltrain *et al*. 2004), which is reflected in the high diversity of their mammalian communities (table 5.1). The climatic changes that took place during the late Pleistocene modified the community structure of the carnivore fauna from southern California. Comparing the carnivore communities from La Brea Tar Pits and Los Angeles, a structural diversity loss arises, with most of the extinct species belonging to one functional group (CFG 1).

All the extinct species from CFG 1 are giant cursorial hipercarnivores (*Smilodon fatalis*, *Panthera atrox* and *Canis dirus*), well adapted to hunt on large prey (Merriam 1912, Stock & Harris 2001). Its extinction would be a consequence of the bottom-up effect of the Pleistocene herbivore megafauna turnover (Ripple & Van Valkenburgh 2010) possibly caused by climatic change and human overhunting (Martin 1973, Martin & Klein 1989, Stuart 1991, Guthrie 2003, Barnosky *et al*. 2004, Robinson *et al*. 2005, Firestone *et al*. 2007, Boulanger & Lyman 2014). These hipercarnivore megapredators were not able to survive in the area when their main feeding source was extinct. The grey wolf is the only representative of the functional group that is present in North America today, but its geographic range is displaced through northern latitudes, where it is associated to high ungulate biomass (Fuller 1989). In any case, Pleistocene grey wolf could be considered an extinct ecomorph specialized in hunting megaprey (Leonard *et al*. 2007), being the northern survivals of the species a different and more generalist form.

The other extinct species is a member of CFG 11, the 'short-faced' bear (*Arctodus simus*). Its extinction would also be linked to the herbivore megafaunal extinction. This giant bear would have a more carnivorous diet than its modern counterparts (Kurtén 1967, Richards *et al*.1996, Barnes *et al*. 2002, Fox-Dobbs *et al*. 2008), even be a strict carnivore and scavenger (Bocherens *et al*. 1995, Matheus 1995, Barnes *et al*. 2002, Donohue *et al*. 2013). Although our results do not support the hipercarnivory in *Arctodus*, the inclusion of large amounts of animal matter in its diet due to active hunt on large prey during cold season (Sorkin 2006, Figueirido *et al*. 2009, 2010), is not dismissed. Additionally, the 'short-faced' bear is phylogenetically close to the South American spectacled bear (*Tremarctos ornatus*), and would present a similar hibernating pattern without seasonal torpor due to the availability of feeding resources throughout all year (Goldstein *et al*. 2008, Krause *et al*. 2008). Consequently, *Arctodus* would present a seasonal diet, including large amounts of vegetable matter during harvesting season, but based on large prey during winter. As in the case of the giant cursorial hipercarnivores from CFG 1, the extinction of its main prey due to Pleistocene faunal turnover would cause a cascade effect, triggering the extinction of this fossil bear.

The remainder members from CFG 11 affected by these climatic shifts are the other ursids, classified as ambulatory omnivores. Both, brown and black bears (*Ursus arctos* and *U. americanus* respectively), have a seasonal diet highly dependent on the availability of fall mast (McLellan *et al.* 1994, Garshelis *et al.* 2005), and its ecological behavior is conditioned by habitat productivity and greenness of temperate and cold forests (Mace *et al.* 1999, Ciarnello *et al.* 2005). Nevertheless, the ecological constrains associated to its behaviour should not impede these species to inhabit the sclerophyllous woodland-shrubland forest, a temperate biome with a seasonal availability of resources. Its presence or absence in the different pits might be a consequence of interspecific competition between these two species. The controlling effect of the brown bear over the black bear (Kendall 1984, Shaffer 1971, Aune 1994, Gunther *et al.* 2002) would have conditioned the presence of the later in the south-western part of California, once the brown bear arrived to the region.

Although the extinction of the giant cursorial hipercarnivores from CFG 1, together with the 'short-faced' bear (CFG 11), and the faunal interchange between the other ursids from CFG 11 deeply changed the community structure of the carnivore associations from California, its absence is not directly related to the landscape evolution throughout late Quaternary. Nonetheless, late Pleistocene and Holocene climatic changes particularly affected to species belonging to CFG 8 and CFG 11. Finally, although CFG 7 remained mostly unaffected by these climatic changes, one species belonging to this functional group, the jaguar (*Panthera onca*), also experienced some limitations in its geographic distribution due to the climatic shifts happened during the last 30,000 years.

The presence of the margay (*Leopardus* cf. *wiedii*), the only scansorial hipercarnivore (CFG 8), and the jaguar (included in CFG 7), together with the absence of the northern raccoon (*Procyon lotor*), seem to be associated to the forested and humid conditions reached during post glacial stages. Its presence in the humid stage of the Holocene seems to be a consequence of the suitable conditions developed during the postglacial period, reducing the ecological constrains imposed by late Pleistocene glaciations (aridity increase and the subsequent reduction of the canopy). The margay is a forest dweller highly associated to the canopy cover of the landscapes (Nowell & Jackson 1996, De Oliveira 1998, Vargas & Huerta 2001, Payan *et al.* 2008, Andrade-Núñez & Mitchell Aide 2010, Carvajal-Villarreal *et al.* 2012). An alteration in the environmental conditions, as the increase of the openness, could produce the displacement of the only representative from CFG 8 from its original areas, due to its low tolerance to deforestation and disturbance of its habitat (Tello 1986, Tewes & Schmildly 1987, Emmons & Feer 1997). The jaguar is strongly conditioned by the humidity of the environment (Mondolfi & Hoogesteijn 1986, Asete *et al.* 2008, Rosas-Rosas *et al.* 2010, Sollmann *et al.* 2012), avoiding arid environments. After the

Last Glacial Maximum, La Brea Tar Pits landscape was a typical arid sclerophyllous woodland-shrubland, which changed to a taiga forest during the postglacial warming (table 5.10). Although both are closed environments, the taiga is a more suitable biome for these species, since it is more humid and densely covered than the sclerophyllous woodland-shrubland (Woodward 2003).

On the contrary, the northern raccoon, although a generalist species capable of living in several landscapes, is highly sensitive to winter length and seasonal availability of food, due to its substantial loose of body weight during winter dormancy (Mech *et al*. 1968, Rosatte *et al*. 1991, Gehrt 2003). Consequently, the long winters associated to the taiga conditions during the postglacial stage might constrain the presence of this omnivore species in the area (Lariviere 2004).

Finally, the environmental changes that took place in the late Pleistocene and Holocene virtually produced no effects over three functional groups (CFG 4, CFG 7 and CFG 9). CFG 4 and CFG 7 are mainly formed by small to medium ambulatory carnivores and hipercarnivores with ground-type locomotion; they survived after the megafauna extinction and appear to be adapted to both, mesic and xeric conditions of the former taiga and the modern sclerophyllous woodland-shrubland. On the other hand, the ringtail (*Bassariscus astutus*), although being a scansorial omnivore from CFG 9, is a ubiquitous species widely distributed through southern North America due to its high adaptability to different environments (Timm *et al*. 2008).

Conclusions

The Carnivore Functional Groups spectra of the mammal communities from La Brea Tar Pits allowed us to identify two rapid swifts in the landscape of California during late Quaternary. First, the sclerophyllous woodland-shrubland established during the late Pleistocene glaciations changed to a humid a taiga forest, due to the increase of the humidity associated to the postglacial warming. These humid and forested conditions remained until arid conditions associated to the sclerophyllous woodland-shrubland found in Los Angeles today were established. Although some of the carnivore mammals from southwestern North America were extinct at the end of the Pleistocene, the ecology of the surviving species remained fairly stable during the last 30,000 years, despite the ecological constrains imposed by the Pleistocene glaciations. These landscape evolution shaped the structure of the carnivore community found in the region. The main effect observed is a structural diversity loss, particularly affecting the species belonging to CFG 1, all of them identified as large cursorial hipercarnivores highly specialized in hunting large herbivores. Nevertheless, the landscape evolution effect over these highly specialized carnivores was associated to a bottom-up effect, probably caused by the Pleistocene herbivore megafauna turnover. On the other hand, the interspecific competition between the black and brown bears appears as the main controlling factor on the presence/absence dynamic of these members from CFG 11. Finally, only the presence of three species, the northern raccoon, the margay and the jaguar, seems to be directly determined by the environmental constrains imposed by the late Quaternary climatic changes. The felids, highly conditioned by the humidity and canopy of the environment, were present in the region only during the humid conditions associated to the Holocene warming. On the contrary, the long length of the winter associated to the taiga, limited the presence of the raccoon, a species highly sensitive to winter length and seasonal availability of food.

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Supplementary data

Supplementary data 5.1. *Fossil specimens measurements to infer the ecology of the species found in La Brea Tar Pits. All the elements were collected from the collection housed in the Page Museum at La Brea Tar Pits, Los Angeles (CA, USA). Measurements from LACMHC Z-53 (Arctodus simus p4) and 20082 (Arctodus simus femur) were taken from Merriam and Stock (1925).*

Number	Specimen Ref.	Species	Anatomical Element
1	LACMHC 1133	*Arctodus simus*	C1
2	LACMHC 1286	*Arctodus simus*	C1
3	LACMHC 50	*Arctodus simus*	C1
4	LACMHC 57504	*Arctodus simus*	C1
5	LACMHC 60453	*Arctodus simus*	C1
6	LACMHC Z-12	*Arctodus simus*	C1
7	LACMHC Z20	*Arctodus simus*	C1
8	LACMHC 1292	*Arctodus simus*	Mandible
9	LACMHC 57516	*Arctodus simus*	Mandible
10	LACMHC 57520	*Arctodus simus*	Mandible
11	LACMHC 57521	*Arctodus simus*	Mandible
12	LACMHC 86	*Arctodus simus*	Mandible
13	LACMHC 88	*Arctodus simus*	Mandible
14	LACMHC 89	*Arctodus simus*	Mandible
15	LACMHC 90	*Arctodus simus*	Mandible
16	LACMHC Z-10	*Arctodus simus*	Mandible
17	LACMHC Z-19	*Arctodus simus*	Mandible
18	LACMHC Z-7	*Arctodus simus*	Mandible
19	LACMHC Z-8 (A)	*Arctodus simus*	Mandible
20	LACMHC Z-9	*Arctodus simus*	Mandible
21	LACMHC Z6	*Arctodus simus*	Mandible
22	LACMHC 1134	*Arctodus simus*	Maxila
23	LACMHC Z-2	*Arctodus simus*	Skull
24	LACMHC Z-4	*Arctodus simus*	Skull
25	LACMHC Z1	*Arctodus simus*	Skull
26	LACMHC 57534	*Arctodus simus*	p4
27	LACMHC 618	*Arctodus simus*	p4
28	LACMHC Z-53	*Arctodus simus*	p4
29	LACMHC 1296	*Arctodus simus*	m3
30	LACMHC 507	*Arctodus simus*	m3
31	LACMHC 57538	*Arctodus simus*	m3
32	LACMHC 57708	*Arctodus simus*	3rd Phalanx Mc III*
33	LACMHC 57709	*Arctodus simus*	3rd Phalanx Mc III*
34	LACMHC 57711	*Arctodus simus*	3rd Phalanx Mc III*
35	R-28678	*Arctodus simus*	3rd Phalanx Mc III*
36	LACMHC 57710	*Arctodus simus*	3rd Phalanx Mc IV*
37	LACMHC Z-140	*Arctodus simus*	3rd Phalanx Mc IV*
38	LACMHC Z-141	*Arctodus simus*	3rd Phalanx Mc IV*
39	GJM 683	*Arctodus simus*	3rd Phalanx Mt III*

Supplementary data 5.1. *Continued*

Number	Specimen Ref.	Species	Anatomical Element
40	LACMHC 57712	*Arctodus simus*	3rd Phalanx Mt III*
41	R-32842	*Arctodus simus*	3rd Phalanx Mt III*
42	R-52510	*Arctodus simus*	3rd Phalanx Mt III*
43	LACMHC 57644	*Arctodus simus*	Astragalus
44	LACMHC 57645	*Arctodus simus*	Astragalus
45	LACMHC 57646	*Arctodus simus*	Astragalus
46	LACMHC 57647	*Arctodus simus*	Astragalus
47	R-40947	*Arctodus simus*	Astragalus
48	Z-111	*Arctodus simus*	Astragalus
49	Z-115	*Arctodus simus*	Astragalus
50	Z-94	*Arctodus simus*	Astragalus
51	Z-96	*Arctodus simus*	Astragalus
52	20082	*Arctodus simus*	Femur
53	LACMHC 57671	*Arctodus simus*	Mt IV
54	R-54077	*Arctodus simus*	Mt IV
55	LACMHC 57684	*Arctodus simus*	1st Phalanx
56	LACMHC 57687	*Arctodus simus*	1st Phalanx
57	LACMHC 57688	*Arctodus simus*	1st Phalanx
58	LACMHC 57689	*Arctodus simus*	1st Phalanx
59	LACMHC 57694	*Arctodus simus*	1st Phalanx
60	LACMHC 57695	*Arctodus simus*	1st Phalanx
61	LACMHC 57697	*Arctodus simus*	1st Phalanx
62	LACMHC 57698	*Arctodus simus*	1st Phalanx
63	LACMHC 57699	*Arctodus simus*	1st Phalanx
64	R-2874	*Arctodus simus*	1st Phalanx
65	S-9681	*Arctodus simus*	1st Phalanx
66	17754	*Arctodus simus*	Mc III
67	21004	*Arctodus simus*	Mc III
68	LACMHC Z-41	*Arctodus simus*	Mc III
69	Z-30	*Arctodus simus*	Ulna
70	20085	*Arctodus simus*	Humerus
71	Z 30	*Arctodus simus*	Humerus
72	Z 32	*Arctodus simus*	Radius
73	Z 31	*Arctodus simus*	Tibia
74	C1 LT PIT3	*Canis dirus*	C1
75	C1 LT PIT4 1	*Canis dirus*	C1
76	C1 PIT 91	*Canis dirus*	C1
77	11947	*Canis dirus*	Mandible
78	2301-L-13	*Canis dirus*	Mandible
79	2301-L-8	*Canis dirus*	Mandible
80	2301-L/R-44	*Canis dirus*	Mandible
81	2301-L&R-26	*Canis dirus*	Mandible

Supplementary data 5.1. *Continued*

Number	Specimen Ref.	Species	Anatomical Element
82	2301-L&R-29	*Canis dirus*	Mandible
83	2301-R-10	*Canis dirus*	Mandible
84	2301-R-11	*Canis dirus*	Mandible
85	2301-R-2	*Canis dirus*	Mandible
86	2301-R-221	*Canis dirus*	Mandible
87	2301-R-24	*Canis dirus*	Mandible
88	2301-R-4	*Canis dirus*	Mandible
89	2301-R-7	*Canis dirus*	Mandible
90	2301-R-8	*Canis dirus*	Mandible
91	28379	*Canis dirus*	Mandible
92	41748	*Canis dirus*	Mandible
93	PMS 952-5	*Canis dirus*	Mandible
94	10402	*Canis dirus*	Skull
95	14795	*Canis dirus*	Skull
96	27080	*Canis dirus*	Skull
97	2300-11	*Canis dirus*	Skull
98	2300-18	*Canis dirus*	Skull
99	2300-22	*Canis dirus*	Skull
100	2300-23	*Canis dirus*	Skull
101	2300-29	*Canis dirus*	Skull
102	2300-31	*Canis dirus*	Skull
103	2300-326	*Canis dirus*	Skull
104	2300-468	*Canis dirus*	Skull
105	LACMHC 126674	*Canis dirus*	Skull
106	PMS 1604-5	*Canis dirus*	Skull
107	H-8488	*Canis dirus*	3rd Phalanx Mc III*
108	H-8492	*Canis dirus*	3rd Phalanx Mc III*
109	H-8510	*Canis dirus*	3rd Phalanx Mc III*
110	H-8831	*Canis dirus*	3rd Phalanx Mc III*
111	H-8832	*Canis dirus*	3rd Phalanx Mc III*
112	H-8841	*Canis dirus*	3rd Phalanx Mc III*
113	H-8844	*Canis dirus*	3rd Phalanx Mc III*
114	H-8891	*Canis dirus*	3rd Phalanx Mc III*
115	H-8893	*Canis dirus*	3rd Phalanx Mc III*
116	H-8928	*Canis dirus*	3rd Phalanx Mc III*
117	PMS 1008-5	*Canis dirus*	3rd Phalanx Mc III*
118	H-8484	*Canis dirus*	3rd Phalanx Mc IV*
119	H-8491	*Canis dirus*	3rd Phalanx Mc IV*
120	H-8495	*Canis dirus*	3rd Phalanx Mc IV*
121	H-8503	*Canis dirus*	3rd Phalanx Mc IV*
122	H-8512	*Canis dirus*	3rd Phalanx Mc IV*
123	H-8517	*Canis dirus*	3rd Phalanx Mc IV*

Supplementary data 5.1. *Continued*

Number	Specimen Ref.	Species	Anatomical Element
124	H-8836	*Canis dirus*	3rd Phalanx Mc IV*
125	PMS 1010-5	*Canis dirus*	3rd Phalanx Mc IV*
126	R-10293	*Canis dirus*	3rd Phalanx Mc IV*
127	R-10394	*Canis dirus*	3rd Phalanx Mc IV*
128	R-28084	*Canis dirus*	3rd Phalanx Mc IV*
129	H-8997	*Canis dirus*	3rd Phalanx Mt III*
130	H-8999	*Canis dirus*	3rd Phalanx Mt III*
131	H-9000	*Canis dirus*	3rd Phalanx Mt III*
132	H-9005	*Canis dirus*	3rd Phalanx Mt III*
133	PMS 1068-5	*Canis dirus*	3rd Phalanx Mt III*
134	R-10713	*Canis dirus*	3rd Phalanx Mt III*
135	R-10779	*Canis dirus*	3rd Phalanx Mt III*
136	R-10995	*Canis dirus*	3rd Phalanx Mt III*
137	R-11159	*Canis dirus*	3rd Phalanx Mt III*
138	R-11256	*Canis dirus*	3rd Phalanx Mt III*
139	R-11536	*Canis dirus*	3rd Phalanx Mt III*
140	F-301	*Canis dirus*	Astragalus
141	F-303	*Canis dirus*	Astragalus
142	F-304	*Canis dirus*	Astragalus
143	F-726	*Canis dirus*	Astragalus
144	F-728	*Canis dirus*	Astragalus
145	F-730	*Canis dirus*	Astragalus
146	F-751	*Canis dirus*	Astragalus
147	PMS 1020-5	*Canis dirus*	Astragalus
148	R-17697	*Canis dirus*	Astragalus
149	R-18663	*Canis dirus*	Astragalus
150	R-23986	*Canis dirus*	Astragalus
151	H-584	*Canis dirus*	Femur
152	H-689	*Canis dirus*	Femur
153	H-698	*Canis dirus*	Femur
154	H-801	*Canis dirus*	Femur
155	H-817	*Canis dirus*	Femur
156	H-827	*Canis dirus*	Femur
157	H-897	*Canis dirus*	Femur
158	PMS 1014-5	*Canis dirus*	Femur
159	R-30472	*Canis dirus*	Femur
160	R-31001	*Canis dirus*	Femur
161	R-33145	*Canis dirus*	Femur
162	D-2989	*Canis dirus*	Mt IV
163	D-2990	*Canis dirus*	Mt IV
164	D-2991	*Canis dirus*	Mt IV
165	D-3004	*Canis dirus*	Mt IV

Supplementary data 5.1. *Continued*

Number	Specimen Ref.	Species	Anatomical Element
166	D-3505	*Canis dirus*	Mt IV
167	D-3516	*Canis dirus*	Mt IV
168	D-3520	*Canis dirus*	Mt IV
169	PMS 1030-5	*Canis dirus*	Mt IV
170	R-10884	*Canis dirus*	Mt IV
171	R-13367	*Canis dirus*	Mt IV
172	R-13403	*Canis dirus*	Mt IV
173	G-1652	*Canis dirus*	1st Phalanx
174	G-2602	*Canis dirus*	1st Phalanx
175	G-3260	*Canis dirus*	1st Phalanx
176	G-3572	*Canis dirus*	1st Phalanx
177	G-7135	*Canis dirus*	1st Phalanx
178	G-7209	*Canis dirus*	1st Phalanx
179	G-7217	*Canis dirus*	1st Phalanx
180	PMS-972-5	*Canis dirus*	1st Phalanx
181	R-15434	*Canis dirus*	1st Phalanx
182	R-26517	*Canis dirus*	1st Phalanx
183	R-29999	*Canis dirus*	1st Phalanx
184	E-145	*Canis dirus*	Mc III
185	E-190	*Canis dirus*	Mc III
186	E-209	*Canis dirus*	Mc III
187	F-9304	*Canis dirus*	Mc III
188	F-9598	*Canis dirus*	Mc III
189	F-9644	*Canis dirus*	Mc III
190	F-9683	*Canis dirus*	Mc III
191	PMS 967-5	*Canis dirus*	Mc III
192	R-12305	*Canis dirus*	Mc III
193	R-13372	*Canis dirus*	Mc III
194	R-35006	*Canis dirus*	Mc III
195	I-6887	*Canis dirus*	Ulna
196	I-6908	*Canis dirus*	Ulna
197	I-6922	*Canis dirus*	Ulna
198	I-7548	*Canis dirus*	Ulna
199	I-7569	*Canis dirus*	Ulna
200	I-7654	*Canis dirus*	Ulna
201	I-7657	*Canis dirus*	Ulna
202	PMS 957-5	*Canis dirus*	Ulna
203	R-13081	*Canis dirus*	Ulna
204	R-28944	*Canis dirus*	Ulna
205	R-28972	*Canis dirus*	Ulna
206	I-6362	*Canis dirus*	Humerus
207	I-6369	*Canis dirus*	Humerus

Supplementary data 5.1. *Continued*

Number	Specimen Ref.	Species	Anatomical Element
208	I-6376	*Canis dirus*	Humerus
209	I-6566	*Canis dirus*	Humerus
210	I-6609	*Canis dirus*	Humerus
211	I-6655	*Canis dirus*	Humerus
212	I-6679	*Canis dirus*	Humerus
213	PMS 955-5	*Canis dirus*	Humerus
214	R-17486	*Canis dirus*	Humerus
215	R-31079	*Canis dirus*	Humerus
216	R-34776	*Canis dirus*	Humerus
217	H-1868	*Canis dirus*	Tibia
218	H-1875	*Canis dirus*	Tibia
219	H-1885	*Canis dirus*	Tibia
220	H-2227	*Canis dirus*	Tibia
221	H-2237	*Canis dirus*	Tibia
222	H-2377	*Canis dirus*	Tibia
223	H-2399	*Canis dirus*	Tibia
224	PMS 1018-5	*Canis dirus*	Tibia
225	R-11659	*Canis dirus*	Tibia
226	R-12135	*Canis dirus*	Tibia
227	R-31101	*Canis dirus*	Tibia
228	LACMHC 125725	*Canis latrans*	C1
229	LACMHC 125726	*Canis latrans*	C1
230	LACMHC 125727	*Canis latrans*	C1
231	LACMHC 125728	*Canis latrans*	C1
232	LACMHC 125729	*Canis latrans*	C1
233	LACMHC 125730	*Canis latrans*	C1
234	LACMHC 125731	*Canis latrans*	C1
235	LACMHC 125732	*Canis latrans*	C1
236	HC 6177	*Canis latrans*	Mandible
237	HC 6181	*Canis latrans*	Mandible
238	HC 6185	*Canis latrans*	Mandible
239	HC 6189	*Canis latrans*	Mandible
240	HC 6191	*Canis latrans*	Mandible
241	HC 6192	*Canis latrans*	Mandible
242	HC 6206	*Canis latrans*	Mandible
243	HC 6207	*Canis latrans*	Mandible
244	HC 6220	*Canis latrans*	Mandible
245	HC 6222	*Canis latrans*	Mandible
246	HC 6224	*Canis latrans*	Mandible
247	LACMHC 56964	*Canis latrans*	Mandible
248	LACMHC 57218	*Canis latrans*	Mandible
249	LACMHC 57219	*Canis latrans*	Mandible

Supplementary data 5.1. *Continued*

Number	Specimen Ref.	Species	Anatomical Element
250	LACMHC 57252	*Canis latrans*	Mandible
251	LACMHC 57371	*Canis latrans*	Mandible
252	3200-19	*Canis latrans*	Skull
253	3200-20	*Canis latrans*	Skull
254	3200-22	*Canis latrans*	Skull
255	3200-4	*Canis latrans*	Skull
256	3200-5	*Canis latrans*	Skull
257	3200-51	*Canis latrans*	Skull
258	3200-59	*Canis latrans*	Skull
259	3200-7	*Canis latrans*	Skull
260	3200-70	*Canis latrans*	Skull
261	3200-9	*Canis latrans*	Skull
262	LACMHC 124644	*Canis latrans*	Skull
263	LACMHC 670	*Canis latrans*	Skull
264	LACMHC 126355	*Canis latrans*	m3
265	LACMHC 126356	*Canis latrans*	m3
266	LACMHC 126357	*Canis latrans*	m3
267	LACMHC 126358	*Canis latrans*	m3
268	LACMHC 126359	*Canis latrans*	m3
269	LACMHC 112677	*Canis latrans*	3rd Phalanx Mc III*
270	LACMHC 121433	*Canis latrans*	3rd Phalanx Mc III*
271	LACMHC 121435	*Canis latrans*	3rd Phalanx Mc III*
272	LACMHC 121437	*Canis latrans*	3rd Phalanx Mc III*
273	LACMHC 121438	*Canis latrans*	3rd Phalanx Mc III*
274	LACMHC 121439	*Canis latrans*	3rd Phalanx Mc III*
275	LACMHC 121440	*Canis latrans*	3rd Phalanx Mc III*
276	LACMHC 121441	*Canis latrans*	3rd Phalanx Mc III*
277	LACMHC 121458	*Canis latrans*	3rd Phalanx Mc III*
278	R-11274	*Canis latrans*	3rd Phalanx Mc III*
279	H-8591	*Canis latrans*	3rd Phalanx Mc IV*
280	H-8703	*Canis latrans*	3rd Phalanx Mc IV*
281	LACMHC 11125	*Canis latrans*	3rd Phalanx Mc IV*
282	LACMHC 121436	*Canis latrans*	3rd Phalanx Mc IV*
283	LACMHC 121442	*Canis latrans*	3rd Phalanx Mc IV*
284	LACMHC 121443	*Canis latrans*	3rd Phalanx Mc IV*
285	LACMHC 121447	*Canis latrans*	3rd Phalanx Mc IV*
286	LACMHC 121456	*Canis latrans*	3rd Phalanx Mc IV*
287	LACMHC 121460	*Canis latrans*	3rd Phalanx Mc IV*
288	R-10336	*Canis latrans*	3rd Phalanx Mc IV*
289	LACMHC 112672	*Canis latrans*	3rd Phalanx Mt III*
290	LACMHC 112673	*Canis latrans*	3rd Phalanx Mt III*
291	LACMHC 112674	*Canis latrans*	3rd Phalanx Mt III*

Supplementary data 5.1. *Continued*

Number	Specimen Ref.	Species	Anatomical Element
292	LACMHC 121444	*Canis latrans*	3rd Phalanx Mt III*
293	LACMHC 121445	*Canis latrans*	3rd Phalanx Mt III*
294	LACMHC 121446	*Canis latrans*	3rd Phalanx Mt III*
295	LACMHC 121459	*Canis latrans*	3rd Phalanx Mt III*
296	LACMHC 95662	*Canis latrans*	3rd Phalanx Mt III*
297	LACMHC 95663	*Canis latrans*	3rd Phalanx Mt III*
298	R-10399	*Canis latrans*	3rd Phalanx Mt III*
299	R-12211	*Canis latrans*	Astragalus
300	R-12273	*Canis latrans*	Astragalus
301	R-13751	*Canis latrans*	Astragalus
302	W-5936	*Canis latrans*	Astragalus
303	W-5947	*Canis latrans*	Astragalus
304	W-5954	*Canis latrans*	Astragalus
305	W-6000	*Canis latrans*	Astragalus
306	W-6064	*Canis latrans*	Astragalus
307	W-6068	*Canis latrans*	Astragalus
308	W-6069	*Canis latrans*	Astragalus
309	LACMHC 112373	*Canis latrans*	Femur
310	W-496	*Canis latrans*	Femur
311	W-497	*Canis latrans*	Femur
312	W-504	*Canis latrans*	Femur
313	W-505	*Canis latrans*	Femur
314	W-506	*Canis latrans*	Femur
315	W-541	*Canis latrans*	Femur
316	W-544	*Canis latrans*	Femur
317	W-545	*Canis latrans*	Femur
318	W-546	*Canis latrans*	Femur
319	W-572	*Canis latrans*	Femur
320	R-13320	*Canis latrans*	Mt IV
321	R-13601	*Canis latrans*	Mt IV
322	R-18920	*Canis latrans*	Mt IV
323	V-383	*Canis latrans*	Mt IV
324	V-384	*Canis latrans*	Mt IV
325	V-385	*Canis latrans*	Mt IV
326	V-386	*Canis latrans*	Mt IV
327	V-498	*Canis latrans*	Mt IV
328	V-499	*Canis latrans*	Mt IV
329	V-500	*Canis latrans*	Mt IV
330	LACMHC 112438	*Canis latrans*	1st Phalanx
331	LACMHC 112439	*Canis latrans*	1st Phalanx
332	LACMHC 112440	*Canis latrans*	1st Phalanx
333	W-7596	*Canis latrans*	1st Phalanx

Supplementary data 5.1. *Continued*

Number	Specimen Ref.	Species	Anatomical Element
334	W-7597	*Canis latrans*	1st Phalanx
335	W-7598	*Canis latrans*	1st Phalanx
336	W-7599	*Canis latrans*	1st Phalanx
337	W-8022	*Canis latrans*	1st Phalanx
338	W-8023	*Canis latrans*	1st Phalanx
339	W-8024	*Canis latrans*	1st Phalanx
340	LACMHC 119431	*Canis latrans*	Mc III
341	R-42461	*Canis latrans*	Mc III
342	W-6675	*Canis latrans*	Mc III
343	W-6676	*Canis latrans*	Mc III
344	W-6677	*Canis latrans*	Mc III
345	W-6678	*Canis latrans*	Mc III
346	W-6787	*Canis latrans*	Mc III
347	W-6788	*Canis latrans*	Mc III
348	W-6789	*Canis latrans*	Mc III
349	W-6802	*Canis latrans*	Mc III
350	LACMHC 118910	*Canis latrans*	Ulna
351	R-17904	*Canis latrans*	Ulna
352	X-9845	*Canis latrans*	Ulna
353	X-9879	*Canis latrans*	Ulna
354	X-9888	*Canis latrans*	Ulna
355	X-9942	*Canis latrans*	Ulna
356	X-9956	*Canis latrans*	Ulna
357	X-9957	*Canis latrans*	Ulna
358	X-9991	*Canis latrans*	Ulna
359	X-9993	*Canis latrans*	Ulna
360	LACMHC 111272	*Canis latrans*	Humerus
361	R-11938	*Canis latrans*	Humerus
362	X-9732	*Canis latrans*	Humerus
363	X-9733	*Canis latrans*	Humerus
364	X-9739	*Canis latrans*	Humerus
365	X-9740	*Canis latrans*	Humerus
366	X-9776	*Canis latrans*	Humerus
367	X-9787	*Canis latrans*	Humerus
368	X-9789	*Canis latrans*	Humerus
369	X-9808	*Canis latrans*	Humerus
370	R-11820	*Canis latrans*	Tibia
371	W-654	*Canis latrans*	Tibia
372	W-713	*Canis latrans*	Tibia
373	W-715	*Canis latrans*	Tibia
374	W-719	*Canis latrans*	Tibia
375	W-722	*Canis latrans*	Tibia

Supplementary data 5.1. *Continued*

Number	Specimen Ref.	Species	Anatomical Element
376	W-750	*Canis latrans*	Tibia
377	W-772	*Canis latrans*	Tibia
378	W-773	*Canis latrans*	Tibia
379	W-803	*Canis latrans*	Tibia
380	LACMHC 126377	*Canis lupus*	C1
381	LACMHC 126379	*Canis lupus*	C1
382	LACMHC 126383	*Canis lupus*	C1
383	LACMHC 126389	*Canis lupus*	C1
384	LACMHC 126394	*Canis lupus*	C1
385	LACMHC 126400	*Canis lupus*	C1
386	LACMHC 126401	*Canis lupus*	C1
387	LACMHC 99833	*Canis lupus*	C1
388	2301-L221	*Canis lupus*	Mandible
389	2301-L470	*Canis lupus*	Mandible
390	2301-L476	*Canis lupus*	Mandible
391	2301-L495	*Canis lupus*	Mandible
392	2301-L498	*Canis lupus*	Mandible
393	2301-R-407	*Canis lupus*	Mandible
394	HC-606	*Canis lupus*	Mandible
395	LACMHC 126413	*Canis lupus*	Mandible
396	LACMHC 126414	*Canis lupus*	Mandible
397	LACMHC 1414	*Canis lupus*	Mandible
398	LACMHC 1435	*Canis lupus*	Mandible
399	LACMHC 314	*Canis lupus*	Mandible
400	LACMHC 54598	*Canis lupus*	Mandible
401	LACMHC 56470	*Canis lupus*	Mandible
402	LACMHC 56471	*Canis lupus*	Mandible
403	LACMHC 56472	*Canis lupus*	Mandible
404	LACMHC 56501	*Canis lupus*	Mandible
405	LACMHC 56637	*Canis lupus*	Mandible
406	LACMHC 56651	*Canis lupus*	Mandible
407	LACMHC 60104	*Canis lupus*	Mandible
408	2300-384	*Canis lupus*	Skull
409	2600-2	*Canis lupus*	Skull
410	2601-R-1	*Canis lupus*	Skull
411	HC-606	*Canis lupus*	Skull
412	HC-607	*Canis lupus*	Skull
413	LACMHC 1414	*Canis lupus*	Skull
414	LACMHC 604	*Canis lupus*	Skull
415	LACMHC 608	*Canis lupus*	Skull
416	LACMHC 609	*Canis lupus*	Skull
417	LACMHC 614	*Canis lupus*	Skull

Supplementary data 5.1. *Continued*

Number	Specimen Ref.	Species	Anatomical Element
418	LACMHC 615	*Canis lupus*	Skull
419	LACMHC 629	*Canis lupus*	Skull
420	F-1527	*Canis lupus*	Astragalus
421	F-1832	*Canis lupus*	Astragalus
422	F-2059	*Canis lupus*	Astragalus
423	F-2235	*Canis lupus*	Astragalus
424	F-365	*Canis lupus*	Astragalus
425	F-764	*Canis lupus*	Astragalus
426	F-810	*Canis lupus*	Astragalus
427	H-663	*Canis lupus*	Femur
428	H-675	*Canis lupus*	Femur
429	H-772	*Canis lupus*	Femur
430	H-774	*Canis lupus*	Femur
431	W-578	*Canis lupus*	Femur
432	D-2064	*Canis lupus*	Mt IV
433	D-3265	*Canis lupus*	Mt IV
434	D-3692	*Canis lupus*	Mt IV
435	LACMHC 99883	*Canis lupus*	Mt IV
436	V-437	*Canis lupus*	Mt IV
437	W-9793	*Canis lupus*	Mt IV
438	G-1344	*Canis lupus*	1st Phalanx
439	G-1584	*Canis lupus*	1st Phalanx
440	G-1603	*Canis lupus*	1st Phalanx
441	G-1788	*Canis lupus*	1st Phalanx
442	G-7113	*Canis lupus*	1st Phalanx
443	G-7247	*Canis lupus*	1st Phalanx
444	G-7301	*Canis lupus*	1st Phalanx
445	LACMHC 126529	*Canis lupus*	3rd Phalanx
446	E-215	*Canis lupus*	Mc III
447	E-24	*Canis lupus*	Mc III
448	F-9432	*Canis lupus*	Mc III
449	F-9437	*Canis lupus*	Mc III
450	F-9468	*Canis lupus*	Mc III
451	F-9469	*Canis lupus*	Mc III
452	W-6799	*Canis lupus*	Mc III
453	I-7394	*Canis lupus*	Ulna
454	I-5786	*Canis lupus*	Humerus
455	I-5820	*Canis lupus*	Humerus
456	I-6039	*Canis lupus*	Humerus
457	I-6367	*Canis lupus*	Humerus
458	I-6386	*Canis lupus*	Humerus
459	I-6613	*Canis lupus*	Humerus

Supplementary data 5.1. *Continued*

Number	Specimen Ref.	Species	Anatomical Element
460	I-6621	*Canis lupus*	Humerus
461	I-6702	*Canis lupus*	Humerus
462	I-9659	*Canis lupus*	Humerus
463	LACMHC 94512	*Canis lupus*	Humerus
464	X-9810	*Canis lupus*	Humerus
465	H-1193	*Canis lupus*	Tibia
466	H-1201	*Canis lupus*	Tibia
467	H-1214	*Canis lupus*	Tibia
468	H-1537	*Canis lupus*	Tibia
469	H-1638	*Canis lupus*	Tibia
470	H-1988	*Canis lupus*	Tibia
471	H-2121	*Canis lupus*	Tibia
472	LACMHC 94559	*Canis lupus*	Tibia
473	LACMHC 94560	*Canis lupus*	Tibia
474	LACMHC 94561	*Canis lupus*	Tibia
475	X-9079	*Leopardus cf. wiedii*	Mandible
476	X-9483	*Leopardus cf. wiedii*	Femur
477	X-9484	*Leopardus cf. wiedii*	Femur
478	X-9479	*Leopardus cf. wiedii*	Ulna
479	X-9478	*Leopardus cf. wiedii*	Humerus
480	X-9485	*Leopardus cf. wiedii*	Tibia
481	X-9486	*Leopardus cf. wiedii*	Tibia
482	X-9488	*Leopardus cf. wiedii*	Tibia
483	LYNX LT C1 PIT 16 (not calalog.)	*Lynx rufus*	C1
484	LYNX C1 PIT 16 (not calalog.)	*Lynx rufus*	C1
485	LYNX C1 PIT 4 (not calalog.)	*Lynx rufus*	C1
486	X9077	*Lynx rufus*	Mandible
487	X9080	*Lynx rufus*	Mandible
488	X9081	*Lynx rufus*	Mandible
489	X9082	*Lynx rufus*	Mandible
490	X9083	*Lynx rufus*	Mandible
491	X9262	*Lynx rufus*	Mandible
492	X9491	*Lynx rufus*	Mandible
493	X9492	*Lynx rufus*	Mandible
494	X9489	*Lynx rufus*	Skull
495	3RD PHLX PIT16 (not calalog.)	*Lynx rufus*	3rd Phalanx Mc III
496	3RD PHLX PIT6909 (not calalog.)	*Lynx rufus*	3rd Phalanx Mc III
497	R-10389	*Lynx rufus*	3rd Phalanx Mt III
498	R-28086	*Lynx rufus*	3rd Phalanx Mt III
499	R-27133	*Lynx rufus*	Astragalus
500	X-9395	*Lynx rufus*	Astragalus

Supplementary data 5.1. *Continued*

Number	Specimen Ref.	Species	Anatomical Element
501	X-9396	*Lynx rufus*	Astragalus
502	X-9397	*Lynx rufus*	Astragalus
503	X-9284	*Lynx rufus*	Femur
504	X-9288	*Lynx rufus*	Femur
505	X-9296	*Lynx rufus*	Femur
506	X-9305	*Lynx rufus*	Femur
507	X-9309	*Lynx rufus*	Femur
508	X-9310	*Lynx rufus*	Femur
509	X-9422	*Lynx rufus*	Mt IV
510	X-9423	*Lynx rufus*	Mt IV
511	X-9425	*Lynx rufus*	Mt IV
512	X-9426	*Lynx rufus*	Mt IV
513	X-9431	*Lynx rufus*	Mt IV
514	X-9432	*Lynx rufus*	Mt IV
515	X-9433	*Lynx rufus*	Mt IV
516	X-9441	*Lynx rufus*	1st Phalanx
517	X-9445	*Lynx rufus*	1st Phalanx
518	X-9446	*Lynx rufus*	1st Phalanx
519	X-9447	*Lynx rufus*	1st Phalanx
520	X-9458	*Lynx rufus*	1st Phalanx
521	X-9460	*Lynx rufus*	1st Phalanx
522	X-9462	*Lynx rufus*	1st Phalanx
523	X-9362	*Lynx rufus*	Mc III
524	X-9365	*Lynx rufus*	Mc III
525	X-9367	*Lynx rufus*	Mc III
526	X-9370	*Lynx rufus*	Mc III
527	X-9372	*Lynx rufus*	Mc III
528	X-9373	*Lynx rufus*	Mc III
529	X-9374	*Lynx rufus*	Mc III
530	X-9375	*Lynx rufus*	Mc III
531	LACMHC 128270	*Mephitis mephitis*	C1
532	LACMHC 128271	*Mephitis mephitis*	C1
533	LACMHC 128272	*Mephitis mephitis*	C1
534	LACMHC 11855	*Mephitis mephitis*	Mandible
535	LACMHC 128238	*Mephitis mephitis*	Mandible
536	LACMHC 128241	*Mephitis mephitis*	Mandible
537	LACMHC 128244	*Mephitis mephitis*	Mandible
538	LACMHC 128245	*Mephitis mephitis*	Mandible
539	LACMHC 128261	*Mephitis mephitis*	Mandible
540	LACMHC 128262	*Mephitis mephitis*	Mandible
541	LACMHC 128264	*Mephitis mephitis*	Mandible
542	V-1124	*Mephitis mephitis*	Mandible

Supplementary data 5.1. *Continued*

Number	Specimen Ref.	Species	Anatomical Element
543	V-1130	*Mephitis mephitis*	Mandible
544	V-1137	*Mephitis mephitis*	Mandible
545	V-1139	*Mephitis mephitis*	Mandible
546	V-1141	*Mephitis mephitis*	Mandible
547	V-1142	*Mephitis mephitis*	Mandible
548	V-1143	*Mephitis mephitis*	Mandible
549	V-1156	*Mephitis mephitis*	Mandible
550	V-1597	*Mephitis mephitis*	Mandible
551	V-1598	*Mephitis mephitis*	Mandible
552	V-1602	*Mephitis mephitis*	Mandible
553	LACMHC 11857	*Mephitis mephitis*	Skull
554	V-1100	*Mephitis mephitis*	Skull
555	V-1107	*Mephitis mephitis*	Skull
556	V-1115	*Mephitis mephitis*	Skull
557	V-1121	*Mephitis mephitis*	Skull
558	V-1585	*Mephitis mephitis*	Skull
559	V-1586	*Mephitis mephitis*	Skull
560	V-1589	*Mephitis mephitis*	Skull
561	V-1592	*Mephitis mephitis*	Skull
562	V-1595	*Mephitis mephitis*	Skull
563	Ast PIT16	*Mephitis mephitis*	Astragalus
564	LACMHC 128354	*Mephitis mephitis*	Astragalus
565	LACMHC 128355	*Mephitis mephitis*	Astragalus
566	LACMHC 128357	*Mephitis mephitis*	Astragalus
567	LACMHC 128335	*Mephitis mephitis*	Femur
568	V-1455	*Mephitis mephitis*	Femur
569	V-1456	*Mephitis mephitis*	Femur
570	V-1457	*Mephitis mephitis*	Femur
571	V-1461	*Mephitis mephitis*	Femur
572	V-1464	*Mephitis mephitis*	Femur
573	V-1465	*Mephitis mephitis*	Femur
574	V-1469	*Mephitis mephitis*	Femur
575	V-1477	*Mephitis mephitis*	Femur
576	V-1478	*Mephitis mephitis*	Femur
577	V-4046	*Mephitis mephitis*	Mt IV
578	V-4095	*Mephitis mephitis*	Mt IV
579	V-4103	*Mephitis mephitis*	Mt IV
580	R-30730	*Mephitis mephitis*	3rd Phalanx
581	LACMHC 128328	*Mephitis mephitis*	Mc III
582	V-1306	*Mephitis mephitis*	Ulna
583	V-1308	*Mephitis mephitis*	Ulna
584	V-1326	*Mephitis mephitis*	Ulna

Supplementary data 5.1. *Continued*

Number	Specimen Ref.	Species	Anatomical Element
585	V-1328	*Mephitis mephitis*	Ulna
586	V-1339	*Mephitis mephitis*	Ulna
587	V-1341	*Mephitis mephitis*	Ulna
588	V-1221	*Mephitis mephitis*	Humerus
589	V-1222	*Mephitis mephitis*	Humerus
590	V-1236	*Mephitis mephitis*	Humerus
591	V-1241	*Mephitis mephitis*	Humerus
592	V-1242	*Mephitis mephitis*	Humerus
593	V-1263	*Mephitis mephitis*	Humerus
594	V-1265	*Mephitis mephitis*	Humerus
595	V-1267	*Mephitis mephitis*	Humerus
596	V-1287	*Mephitis mephitis*	Humerus
597	V-1288	*Mephitis mephitis*	Humerus
598	LACMHC 128343	*Mephitis mephitis*	Tibia
599	V-1526	*Mephitis mephitis*	Tibia
600	V-1530	*Mephitis mephitis*	Tibia
601	V-1532	*Mephitis mephitis*	Tibia
602	V-1536	*Mephitis mephitis*	Tibia
603	V-1553	*Mephitis mephitis*	Tibia
604	V-1554	*Mephitis mephitis*	Tibia
605	V-1555	*Mephitis mephitis*	Tibia
606	V-1557	*Mephitis mephitis*	Tibia
607	V-1572	*Mephitis mephitis*	Tibia
608	LACMHC 11826	*Mustela frenata*	m1
609	LACMHC 11827	*Mustela frenata*	m1
610	LACMHC 128390	*Mustela frenata*	Mandible
611	LACMHC 128391	*Mustela frenata*	Mandible
612	LACMHC 128392	*Mustela frenata*	Mandible
613	LACMHC 128393	*Mustela frenata*	Mandible
614	LACMHC 128394	*Mustela frenata*	Mandible
615	LACMHC 128395	*Mustela frenata*	Mandible
616	LACMHC 128398	*Mustela frenata*	Mandible
617	LACMHC 128399	*Mustela frenata*	Mandible
618	LACMHC 128400	*Mustela frenata*	Mandible
619	LACMHC 128401	*Mustela frenata*	Mandible
620	V-1638	*Mustela frenata*	Mandible
621	V-1639	*Mustela frenata*	Mandible
622	V-1640	*Mustela frenata*	Mandible
623	V-1641	*Mustela frenata*	Mandible
624	LACMHC 11849	*Mustela frenata*	Skull
625	LACMHC 11851	*Mustela frenata*	Skull
626	LACMHC 11853	*Mustela frenata*	Skull

Supplementary data 5.1. *Continued*

Number	Specimen Ref.	Species	Anatomical Element
627	V-1613	*Mustela frenata*	Skull
628	V-1622	*Mustela frenata*	Skull
629	V-1625	*Mustela frenata*	Skull
630	V-1626	*Mustela frenata*	Skull
631	V-1631	*Mustela frenata*	Skull
632	V-1632	*Mustela frenata*	Skull
633	V-1633	*Mustela frenata*	Skull
634	V-1634	*Mustela frenata*	Skull
635	V-1636	*Mustela frenata*	Skull
636	LACMHC 11848	*Mustela frenata*	Femur
637	LACMHC 128418	*Mustela frenata*	Femur
638	V-1654	*Mustela frenata*	Femur
639	V-1654	*Mustela frenata*	Femur
640	V-1661	*Mustela frenata*	Femur
641	V-1661	*Mustela frenata*	Femur
642	V-1663	*Mustela frenata*	Femur
643	V-1663	*Mustela frenata*	Femur
644	V-1664	*Mustela frenata*	Femur
645	V-1664	*Mustela frenata*	Femur
646	V-1665	*Mustela frenata*	Femur
647	V-1665	*Mustela frenata*	Femur
648	V-1666	*Mustela frenata*	Femur
649	V-1666	*Mustela frenata*	Femur
650	V-1667	*Mustela frenata*	Femur
651	V-1667	*Mustela frenata*	Femur
652	V-1668	*Mustela frenata*	Femur
653	V-1668	*Mustela frenata*	Femur
654	R-46984	*Mustela frenata*	1st Phalanx
655	LACMHC 128409	*Mustela frenata*	Ulna
656	LACMHC 128410	*Mustela frenata*	Ulna
657	LACMHC 128406	*Mustela frenata*	Humerus
658	V-1643	*Mustela frenata*	Humerus
659	V-1644	*Mustela frenata*	Humerus
660	V-1645	*Mustela frenata*	Humerus
661	V-1646	*Mustela frenata*	Humerus
662	V-1647	*Mustela frenata*	Humerus
663	V-1648	*Mustela frenata*	Humerus
664	V-1649	*Mustela frenata*	Humerus
665	V-1650	*Mustela frenata*	Humerus
666	V-1651	*Mustela frenata*	Humerus
667	LACMHC 128422	*Mustela frenata*	Tibia
668	V-1669	*Mustela frenata*	Tibia

Supplementary data 5.1. *Continued*

Number	Specimen Ref.	Species	Anatomical Element
669	V-1670	*Mustela frenata*	Tibia
670	HC 601	*Panthera atrox*	m1
671	LACMHC 10167	*Panthera atrox*	C1
672	LACMHC 17132	*Panthera atrox*	C1
673	LACMHC 179	*Panthera atrox*	C1
674	LACMHC 53	*Panthera atrox*	C1
675	LACMHC 53641	*Panthera atrox*	C1
676	LACMHC 653	*Panthera atrox*	C1
677	2901-L/R-5 (LACMHC 1)	*Panthera atrox*	Mandible
678	LACMHC 286	*Panthera atrox*	Mandible
679	LACMHC 2901-6	*Panthera atrox*	Mandible
680	LACMHC 585	*Panthera atrox*	Mandible
681	LACMHC 589	*Panthera atrox*	Mandible
682	LACMHC 591	*Panthera atrox*	Mandible
683	LACMHC 593	*Panthera atrox*	Mandible
684	LACMHC 595	*Panthera atrox*	Mandible
685	LACMHC 597	*Panthera atrox*	Mandible
686	LACMHC 599	*Panthera atrox*	Mandible
687	LACMHC 65	*Panthera atrox*	Mandible
688	LACMHC 2900-10	*Panthera atrox*	Skull
689	LACMHC 2900-12	*Panthera atrox*	Skull
690	LACMHC 2900-15	*Panthera atrox*	Skull
691	LACMHC 2900-16	*Panthera atrox*	Skull
692	LACMHC 2900-17	*Panthera atrox*	Skull
693	LACMHC 2900-19	*Panthera atrox*	Skull
694	LACMHC 2900-20	*Panthera atrox*	Skull
695	LACMHC 2900-5	*Panthera atrox*	Skull
696	LACMHC 2900-6	*Panthera atrox*	Skull
697	LACMHC 2900-7	*Panthera atrox*	Skull
698	LACMHC 2900-8	*Panthera atrox*	Skull
699	LACMHC 2900-9	*Panthera atrox*	Skull
700	LACMHC 109272	*Panthera atrox*	3rd Phalanx Mc III
701	LACMHC 109616	*Panthera atrox*	3rd Phalanx Mc III
702	LACMHC 109718	*Panthera atrox*	3rd Phalanx Mc III
703	LACMHC 109849	*Panthera atrox*	3rd Phalanx Mc III
704	LACMHC 109879	*Panthera atrox*	3rd Phalanx Mc III
705	LACMHC 115969	*Panthera atrox*	3rd Phalanx Mc III
706	LACMHC 115970	*Panthera atrox*	3rd Phalanx Mc III
707	R-6928	*Panthera atrox*	3rd Phalanx Mc III
708	R-7090	*Panthera atrox*	3rd Phalanx Mc III
709	R-7569	*Panthera atrox*	3rd Phalanx Mc III
710	LACMHC 109137	*Panthera atrox*	3rd Phalanx Mc IV

Supplementary data 5.1. *Continued*

Number	Specimen Ref.	Species	Anatomical Element
711	LACMHC 109505	*Panthera atrox*	3rd Phalanx Mc IV
712	LACMHC 109522	*Panthera atrox*	3rd Phalanx Mc IV
713	LACMHC 109714	*Panthera atrox*	3rd Phalanx Mc IV
714	LACMHC 109914	*Panthera atrox*	3rd Phalanx Mc IV
715	LACMHC 109974	*Panthera atrox*	3rd Phalanx Mc IV
716	LACMHC 111956	*Panthera atrox*	3rd Phalanx Mc IV
717	LACMHC 115975	*Panthera atrox*	3rd Phalanx Mc IV
718	R-7326	*Panthera atrox*	3rd Phalanx Mc IV
719	R-7466	*Panthera atrox*	3rd Phalanx Mc IV
720	LACMHC 108499	*Panthera atrox*	3rd Phalanx Mt III
721	LACMHC 109190	*Panthera atrox*	3rd Phalanx Mt III
722	LACMHC 109781	*Panthera atrox*	3rd Phalanx Mt III
723	LACMHC 110522	*Panthera atrox*	3rd Phalanx Mt III
724	LACMHC 115981	*Panthera atrox*	3rd Phalanx Mt III
725	R-7576	*Panthera atrox*	3rd Phalanx Mt III
726	R-7678	*Panthera atrox*	3rd Phalanx Mt III
727	R-8417	*Panthera atrox*	3rd Phalanx Mt III
728	R-8708	*Panthera atrox*	3rd Phalanx Mt III
729	R-8768	*Panthera atrox*	3rd Phalanx Mt III
730	LACMHC 15450	*Panthera atrox*	Astragalus
731	LACMHC 15452	*Panthera atrox*	Astragalus
732	LACMHC 15456	*Panthera atrox*	Astragalus
733	LACMHC 15459	*Panthera atrox*	Astragalus
734	LACMHC 15467	*Panthera atrox*	Astragalus
735	LACMHC 15468	*Panthera atrox*	Astragalus
736	LACMHC 15469	*Panthera atrox*	Astragalus
737	LACMHC 15482	*Panthera atrox*	Astragalus
738	R-24353	*Panthera atrox*	Astragalus
739	R-34498	*Panthera atrox*	Astragalus
740	2907-R-10	*Panthera atrox*	Femur
741	2907-R-11	*Panthera atrox*	Femur
742	LACMHC 15260	*Panthera atrox*	Femur
743	LACMHC 90574	*Panthera atrox*	Femur
744	X-7123	*Panthera atrox*	Femur
745	X-7143	*Panthera atrox*	Femur
746	X-7144	*Panthera atrox*	Femur
747	X-7155	*Panthera atrox*	Femur
748	X-7190	*Panthera atrox*	Femur
749	X-7192	*Panthera atrox*	Femur
750	LACMHC 16061	*Panthera atrox*	Mt IV
751	LACMHC 16062	*Panthera atrox*	Mt IV
752	LACMHC 59952	*Panthera atrox*	Mt IV

Supplementary data 5.1. *Continued*

Number	Specimen Ref.	Species	Anatomical Element
753	X-5342	*Panthera atrox*	Mt IV
754	X-5343	*Panthera atrox*	Mt IV
755	X-5355	*Panthera atrox*	Mt IV
756	X-5356	*Panthera atrox*	Mt IV
757	X-5476	*Panthera atrox*	Mt IV
758	X-5479	*Panthera atrox*	Mt IV
759	X-5492	*Panthera atrox*	Mt IV
760	LACMHC 16169	*Panthera atrox*	1st Phalanx
761	LACMHC 16177	*Panthera atrox*	1st Phalanx
762	LACMHC 16184	*Panthera atrox*	1st Phalanx
763	LACMHC 16188	*Panthera atrox*	1st Phalanx
764	LACMHC 16319	*Panthera atrox*	1st Phalanx
765	LACMHC 16327	*Panthera atrox*	1st Phalanx
766	LACMHC 16331	*Panthera atrox*	1st Phalanx
767	LACMHC 16458	*Panthera atrox*	1st Phalanx
768	LACMHC 16468	*Panthera atrox*	1st Phalanx
769	R-12390	*Panthera atrox*	1st Phalanx
770	R-48725	*Panthera atrox*	Mc III
771	X-5040	*Panthera atrox*	Mc III
772	X-5042	*Panthera atrox*	Mc III
773	X-5170	*Panthera atrox*	Mc III
774	X-5171	*Panthera atrox*	Mc III
775	X-5173	*Panthera atrox*	Mc III
776	X-5177	*Panthera atrox*	Mc III
777	X-5179	*Panthera atrox*	Mc III
778	X-5180	*Panthera atrox*	Mc III
779	X-5192	*Panthera atrox*	Mc III
780	2905-R-8	*Panthera atrox*	Ulna
781	LACMHC 14621	*Panthera atrox*	Ulna
782	X-5054	*Panthera atrox*	Ulna
783	X-6989	*Panthera atrox*	Ulna
784	X-7006	*Panthera atrox*	Ulna
785	X-7016	*Panthera atrox*	Ulna
786	X-7019	*Panthera atrox*	Ulna
787	X-7028	*Panthera atrox*	Ulna
788	X-7044	*Panthera atrox*	Ulna
789	X-7052	*Panthera atrox*	Ulna
790	LACMHC 53321	*Panthera onca*	C1
791	LACMHC 56466	*Panthera onca*	C1
792	LACMHC 56467	*Panthera onca*	C1
793	LACMHC 56468	*Panthera onca*	C1
794	LACMHC 17023	*Panthera onca*	Mandible

Supplementary data 5.1. *Continued*

Number	Specimen Ref.	Species	Anatomical Element
795	LACMHC 32706	*Panthera onca*	Mandible
796	LACMHC 1436	*Panthera onca*	Maxila
797	LACMHC 59961	*Panthera onca*	Astragalus
798	X-8848	*Panthera onca*	Femur
799	LACMHC 6938	*Panthera onca*	Mc III
800	T-1215	*Panthera onca*	Mc III
801	m1 ACAD	*Puma concolor*	m1
802	13/(F-11,12 (1/2))	*Puma concolor*	C1
803	16D C1	*Puma concolor*	C1
804	X-8627	*Puma concolor*	C1
805	13/(F, 11,11 (1/2, 1))	*Puma concolor*	Mandible
806	HC-6319	*Puma concolor*	Mandible
807	L2100-53-209	*Puma concolor*	Mandible
808	UCMP 2050/21572	*Puma concolor*	Mandible
809	X-9465	*Puma concolor*	Mandible
810	X-9466	*Puma concolor*	Mandible
811	X-9467	*Puma concolor*	Mandible
812	X-9468	*Puma concolor*	Mandible
813	X-9469	*Puma concolor*	Mandible
814	X-9470	*Puma concolor*	Mandible
815	X-9472	*Puma concolor*	Mandible
816	X-9473	*Puma concolor*	Mandible
817	X-9474	*Puma concolor*	Mandible
818	LACMHC 91 (X-8629)	*Puma concolor*	Skull
819	LACMHC 109679	*Puma concolor*	3rd Phalanx Mc III
820	LACMHC 110543	*Puma concolor*	3rd Phalanx Mc III
821	R-10593	*Puma concolor*	3rd Phalanx Mc III
822	R-10600	*Puma concolor*	3rd Phalanx Mc III
823	LACMHC 109683	*Puma concolor*	3rd Phalanx Mc IV
824	LACMHC 110369	*Puma concolor*	3rd Phalanx Mc IV
825	LACMHC 110371	*Puma concolor*	3rd Phalanx Mc IV
826	LACMHC 110702	*Puma concolor*	3rd Phalanx Mt III
827	X-9071	*Puma concolor*	3rd Phalanx Mt III
828	X-8988	*Puma concolor*	Astragalus
829	X-8990	*Puma concolor*	Astragalus
830	X-8991	*Puma concolor*	Astragalus
831	X-8992	*Puma concolor*	Astragalus
832	X-8993	*Puma concolor*	Astragalus
833	X-8994	*Puma concolor*	Astragalus
834	X-8995	*Puma concolor*	Astragalus
835	X-8846	*Puma concolor*	Femur
836	X-9020	*Puma concolor*	Mt IV

Supplementary data 5.1. *Continued*

Number	Specimen Ref.	Species	Anatomical Element
837	X-9021	*Puma concolor*	Mt IV
838	G-5259	*Puma concolor*	1st Phalanx
839	G-6497	*Puma concolor*	1st Phalanx
840	G-6501	*Puma concolor*	1st Phalanx
841	G-7134	*Puma concolor*	1st Phalanx
842	G-9899	*Puma concolor*	1st Phalanx
843	LACMHC 59739	*Puma concolor*	1st Phalanx
844	LACMHC 85588	*Puma concolor*	1st Phalanx
845	X-9054	*Puma concolor*	1st Phalanx
846	X-9057	*Puma concolor*	1st Phalanx
847	X-9062	*Puma concolor*	1st Phalanx
848	LACMHC 84639	*Puma concolor*	Mc III
849	X-8949	*Puma concolor*	Mc III
850	X-8951	*Puma concolor*	Mc III
851	X-8952	*Puma concolor*	Mc III
852	X-8953	*Puma concolor*	Mc III
853	X-8956	*Puma concolor*	Mc III
854	X-8957	*Puma concolor*	Mc III
855	X-8958	*Puma concolor*	Mc III
856	X-8959	*Puma concolor*	Mc III
857	X-9023	*Puma concolor*	Mc III
858	X-8811	*Puma concolor*	Ulna
859	X-8813	*Puma concolor*	Ulna
860	X-8819	*Puma concolor*	Ulna
861	PMS 2-1	*Smilodon fatalis*	m1
862	LACMHC 218	*Smilodon fatalis*	C1
863	LACMHC 219	*Smilodon fatalis*	C1
864	LACMHC 237	*Smilodon fatalis*	C1
865	LACMHC 59	*Smilodon fatalis*	C1
866	LACMHC 631	*Smilodon fatalis*	C1
867	17277	*Smilodon fatalis*	Mandible
868	18747	*Smilodon fatalis*	Mandible
869	20274	*Smilodon fatalis*	Mandible
870	2002-L/R-27	*Smilodon fatalis*	Mandible
871	2002-L/R-39	*Smilodon fatalis*	Mandible
872	2002-L/R-44	*Smilodon fatalis*	Mandible
873	2002-L/R-46	*Smilodon fatalis*	Mandible
874	2002-L/R-59	*Smilodon fatalis*	Mandible
875	2002-L/R-61	*Smilodon fatalis*	Mandible
876	2002-L/R-71	*Smilodon fatalis*	Mandible
877	10688	*Smilodon fatalis*	Skull
878	10864	*Smilodon fatalis*	Skull

Supplementary data 5.1. *Continued*

Number	Specimen Ref.	Species	Anatomical Element
879	20273	*Smilodon fatalis*	Skull
880	2001-106	*Smilodon fatalis*	Skull
881	2001-118	*Smilodon fatalis*	Skull
882	2001-123	*Smilodon fatalis*	Skull
883	2001-125	*Smilodon fatalis*	Skull
884	2001-138	*Smilodon fatalis*	Skull
885	2001-140	*Smilodon fatalis*	Skull
886	2001-150	*Smilodon fatalis*	Skull
887	PMS 1-1	*Smilodon fatalis*	Skull
888	LACMHC 108522	*Smilodon fatalis*	3rd Phalanx Mc III
889	LACMHC 109088	*Smilodon fatalis*	3rd Phalanx Mc III
890	LACMHC 109172	*Smilodon fatalis*	3rd Phalanx Mc III
891	LACMHC 110199	*Smilodon fatalis*	3rd Phalanx Mc III
892	PMS 60-1	*Smilodon fatalis*	3rd Phalanx Mc III
893	R-6952	*Smilodon fatalis*	3rd Phalanx Mc III
894	R-7383	*Smilodon fatalis*	3rd Phalanx Mc III
895	R-8162	*Smilodon fatalis*	3rd Phalanx Mc III
896	R-8691	*Smilodon fatalis*	3rd Phalanx Mc III
897	R-8711	*Smilodon fatalis*	3rd Phalanx Mc III
898	R-8736	*Smilodon fatalis*	3rd Phalanx Mc III
899	PMS 61-1	*Smilodon fatalis*	3rd Phalanx Mc IV
900	R-7378	*Smilodon fatalis*	3rd Phalanx Mc IV
901	R-7510	*Smilodon fatalis*	3rd Phalanx Mc IV
902	R-7615	*Smilodon fatalis*	3rd Phalanx Mc IV
903	R-8081	*Smilodon fatalis*	3rd Phalanx Mc IV
904	R-8188	*Smilodon fatalis*	3rd Phalanx Mc IV
905	R-8376	*Smilodon fatalis*	3rd Phalanx Mc IV
906	R-8384	*Smilodon fatalis*	3rd Phalanx Mc IV
907	R-8693	*Smilodon fatalis*	3rd Phalanx Mc IV
908	R-8697	*Smilodon fatalis*	3rd Phalanx Mc IV
909	R-8730	*Smilodon fatalis*	3rd Phalanx Mc IV
910	LACMHC 110227	*Smilodon fatalis*	3rd Phalanx Mt III
911	PMS 105-1	*Smilodon fatalis*	3rd Phalanx Mt III
912	R-7132	*Smilodon fatalis*	3rd Phalanx Mt III
913	R-7783	*Smilodon fatalis*	3rd Phalanx Mt III
914	R-8448	*Smilodon fatalis*	3rd Phalanx Mt III
915	R-8511	*Smilodon fatalis*	3rd Phalanx Mt III
916	R-8554	*Smilodon fatalis*	3rd Phalanx Mt III
917	R-8598	*Smilodon fatalis*	3rd Phalanx Mt III
918	R-8707	*Smilodon fatalis*	3rd Phalanx Mt III
919	R-8722	*Smilodon fatalis*	3rd Phalanx Mt III
920	R-8748	*Smilodon fatalis*	3rd Phalanx Mt III

Supplementary data 5.1. *Continued*

Number	Specimen Ref.	Species	Anatomical Element
921	T-5236	*Smilodon fatalis*	Astragalus
922	T-5237	*Smilodon fatalis*	Astragalus
923	T-5602	*Smilodon fatalis*	Astragalus
924	T-5606	*Smilodon fatalis*	Astragalus
925	T-5612	*Smilodon fatalis*	Astragalus
926	T-5798	*Smilodon fatalis*	Astragalus
927	T-5834	*Smilodon fatalis*	Astragalus
928	T-5849	*Smilodon fatalis*	Astragalus
929	T-5877	*Smilodon fatalis*	Astragalus
930	T-6070	*Smilodon fatalis*	Astragalus
931	11349	*Smilodon fatalis*	Femur
932	15239	*Smilodon fatalis*	Femur
933	27626	*Smilodon fatalis*	Femur
934	K-3576	*Smilodon fatalis*	Femur
935	K-3592	*Smilodon fatalis*	Femur
936	K-3666	*Smilodon fatalis*	Femur
937	K-3748	*Smilodon fatalis*	Femur
938	K-3755	*Smilodon fatalis*	Femur
939	K-3766	*Smilodon fatalis*	Femur
940	K-3767	*Smilodon fatalis*	Femur
941	PMS 80-1	*Smilodon fatalis*	Femur
942	PMS 93-1	*Smilodon fatalis*	Mt IV
943	R-10125	*Smilodon fatalis*	Mt IV
944	R-11853	*Smilodon fatalis*	Mt IV
945	R-12820	*Smilodon fatalis*	Mt IV
946	U-9055	*Smilodon fatalis*	Mt IV
947	U-9085	*Smilodon fatalis*	Mt IV
948	U-9127	*Smilodon fatalis*	Mt IV
949	U-9139	*Smilodon fatalis*	Mt IV
950	U-9396	*Smilodon fatalis*	Mt IV
951	U-9413	*Smilodon fatalis*	Mt IV
952	U-9414	*Smilodon fatalis*	Mt IV
953	LACMHC 50564	*Smilodon fatalis*	1st Phalanx
954	LACMHC 50583	*Smilodon fatalis*	1st Phalanx
955	LACMHC 50858	*Smilodon fatalis*	1st Phalanx
956	LACMHC 50860	*Smilodon fatalis*	1st Phalanx
957	LACMHC 50867	*Smilodon fatalis*	1st Phalanx
958	LACMHC 61158	*Smilodon fatalis*	1st Phalanx
959	PMS 51-1	*Smilodon fatalis*	1st Phalanx
960	R-931	*Smilodon fatalis*	1st Phalanx
961	S-8262	*Smilodon fatalis*	1st Phalanx
962	S-8265	*Smilodon fatalis*	1st Phalanx

Supplementary data 5.1. *Continued*

Number	Specimen Ref.	Species	Anatomical Element
963	S-8511	*Smilodon fatalis*	1st Phalanx
964	PMS 46-1	*Smilodon fatalis*	Mc III
965	U-3471	*Smilodon fatalis*	Mc III
966	U-3506	*Smilodon fatalis*	Mc III
967	U-3535	*Smilodon fatalis*	Mc III
968	U-3576	*Smilodon fatalis*	Mc III
969	U-3817	*Smilodon fatalis*	Mc III
970	U-3846	*Smilodon fatalis*	Mc III
971	U-3847	*Smilodon fatalis*	Mc III
972	U-4042	*Smilodon fatalis*	Mc III
973	U-4044	*Smilodon fatalis*	Mc III
974	U-4045	*Smilodon fatalis*	Mc III
975	K-1421	*Smilodon fatalis*	Ulna
976	K-1429	*Smilodon fatalis*	Ulna
977	K-1432	*Smilodon fatalis*	Ulna
978	K-1520	*Smilodon fatalis*	Ulna
979	K-1526	*Smilodon fatalis*	Ulna
980	K-1530	*Smilodon fatalis*	Ulna
981	K-1531	*Smilodon fatalis*	Ulna
982	K-984	*Smilodon fatalis*	Ulna
983	K-985	*Smilodon fatalis*	Ulna
984	LACMHC 53346	*Smilodon fatalis*	Ulna
985	PMS 5-1	*Smilodon fatalis*	Ulna
986	LACMHC 127752	*Spilogale putorius*	m1
987	LACMHC 127744	*Spilogale putorius*	C1
988	LACMHC 127749	*Spilogale putorius*	C1
989	LACMHC 127751	*Spilogale putorius*	Mandible
990	V-1612	*Spilogale putorius*	Mandible
991	LACMHC 62501	*Spilogale putorius*	Skull
992	V-1607	*Spilogale putorius*	Skull
993	V-1609	*Spilogale putorius*	Skull
994	V-1610	*Spilogale putorius*	Skull
995	LACMHC 127747	*Spilogale putorius*	M1+M2
996	LACMHC 127753	*Spilogale putorius*	Femur
997	R-16710	*Spilogale putorius*	Ulna
998	V-1305	*Spilogale putorius*	Ulna
999	V-1219	*Spilogale putorius*	Humerus
1000	V-1220	*Spilogale putorius*	Humerus
1001	V-1259	*Spilogale putorius*	Humerus
1002	V-1261	*Spilogale putorius*	Humerus
1003	TIB ND (not calalog.)	*Spilogale putorius*	Tibia
1004	V-1522	*Spilogale putorius*	Tibia

Supplementary data 5.1. *Continued*

Number	Specimen Ref.	Species	Anatomical Element
1005	V-1523	*Spilogale putorius*	Tibia
1006	V-1546	*Spilogale putorius*	Tibia
1007	V-1548	*Spilogale putorius*	Tibia
1008	V-1549	*Spilogale putorius*	Tibia
1009	Academy	*Taxidea taxus*	m1
1010	LACMHC 11523	*Taxidea taxus*	m1
1011	LACMHC 11524	*Taxidea taxus*	m1
1012	LACMHC 11525	*Taxidea taxus*	m1
1013	LACMHC 11526	*Taxidea taxus*	m1
1014	LACMHC 11498	*Taxidea taxus*	C1
1015	LACMHC 11499	*Taxidea taxus*	C1
1016	LACMHC 11500	*Taxidea taxus*	C1
1017	LACMHC 11501	*Taxidea taxus*	C1
1018	LACMHC 128097	*Taxidea taxus*	C1
1019	LACMHC 128098	*Taxidea taxus*	C1
1020	LACMHC 128099	*Taxidea taxus*	C1
1021	LACMHC 11510	*Taxidea taxus*	Mandible
1022	LACMHC 11512	*Taxidea taxus*	Mandible
1023	LACMHC 11517	*Taxidea taxus*	Mandible
1024	P23 6801	*Taxidea taxus*	Mandible
1025	V-804	*Taxidea taxus*	Mandible
1026	3 PH PIT ND (not calalog.)	*Taxidea taxus*	3rd Phalanx Mc III*
1027	LACMHC 9907	*Taxidea taxus*	3rd Phalanx Mc III*
1028	R-49483	*Taxidea taxus*	3rd Phalanx Mc III*
1029	LACMHC 9908	*Taxidea taxus*	3rd Phalanx Mc IV*
1030	LACMHC 9909	*Taxidea taxus*	3rd Phalanx Mc IV*
1031	R-13098	*Taxidea taxus*	3rd Phalanx Mc IV*
1032	3 PH PIT 6909 (not calalog.)	*Taxidea taxus*	3rd Phalanx Mt III*
1033	E-7374	*Taxidea taxus*	3rd Phalanx Mt III*
1034	R-15468	*Taxidea taxus*	3rd Phalanx Mt III*
1035	V-1065	*Taxidea taxus*	Astragalus
1036	LACMHC 9569	*Taxidea taxus*	Femur
1037	LACMHC 9570	*Taxidea taxus*	Femur
1038	LACMHC 9904	*Taxidea taxus*	Femur
1039	V-1004	*Taxidea taxus*	Femur
1040	V-1007	*Taxidea taxus*	Femur
1041	V-1008	*Taxidea taxus*	Femur
1042	V-1009	*Taxidea taxus*	Femur
1043	V-1010	*Taxidea taxus*	Femur
1044	V-1013	*Taxidea taxus*	Femur
1045	V-1014	*Taxidea taxus*	Femur
1046	R-42162	*Taxidea taxus*	Mt IV

Supplementary data 5.1. *Continued*

Number	Specimen Ref.	Species	Anatomical Element
1047	V-1066	*Taxidea taxus*	Mt IV
1048	V-1067	*Taxidea taxus*	Mt IV
1049	V-1068	*Taxidea taxus*	Mt IV
1050	LACMHC 128113	*Taxidea taxus*	1st Phalanx
1051	R-21781	*Taxidea taxus*	1st Phalanx
1052	V-1053	*Taxidea taxus*	1st Phalanx
1053	V-1054	*Taxidea taxus*	1st Phalanx
1054	V-1055	*Taxidea taxus*	1st Phalanx
1055	V-1056	*Taxidea taxus*	1st Phalanx
1056	V-1060	*Taxidea taxus*	1st Phalanx
1057	V-1061	*Taxidea taxus*	1st Phalanx
1058	LACMHC 128090	*Taxidea taxus*	Mc III
1059	V-1045	*Taxidea taxus*	Mc III
1060	V-1049	*Taxidea taxus*	Mc III
1061	V-1050	*Taxidea taxus*	Mc III
1062	V-941	*Taxidea taxus*	Ulna
1063	V-942	*Taxidea taxus*	Ulna
1064	V-943	*Taxidea taxus*	Ulna
1065	V-949	*Taxidea taxus*	Ulna
1066	V-951	*Taxidea taxus*	Ulna
1067	V-952	*Taxidea taxus*	Ulna
1068	V-953	*Taxidea taxus*	Ulna
1069	LACMHC 9554	*Taxidea taxus*	Humerus
1070	LACMHC 9559	*Taxidea taxus*	Humerus
1071	V-917	*Taxidea taxus*	Humerus
1072	V-918	*Taxidea taxus*	Humerus
1073	V-920	*Taxidea taxus*	Humerus
1074	V-921	*Taxidea taxus*	Humerus
1075	V-922	*Taxidea taxus*	Humerus
1076	V-925	*Taxidea taxus*	Humerus
1077	V-928	*Taxidea taxus*	Humerus
1078	LACMHC 9573	*Taxidea taxus*	Tibia
1079	V-1025	*Taxidea taxus*	Tibia
1080	V-1026	*Taxidea taxus*	Tibia
1081	V-1028	*Taxidea taxus*	Tibia
1082	V-1029	*Taxidea taxus*	Tibia
1083	V-1030	*Taxidea taxus*	Tibia
1084	V-1031	*Taxidea taxus*	Tibia
1085	V-1032	*Taxidea taxus*	Tibia
1086	V-1033	*Taxidea taxus*	Tibia
1087	V-1034	*Taxidea taxus*	Tibia
1088	LACMHC 58022	*Urocyon cinenreoargenteus*	m1

Supplementary data 5.1. *Continued*

Number	Specimen Ref.	Species	Anatomical Element
1089	LACMHC 58048	*Urocyon cinenreoargenteus*	m1
1116	LACMHC 58050	*Urocyon cinenreoargenteus*	m2
1093	LACMHC 58037	*Urocyon cinenreoargenteus*	Mandible
1094	LACMHC 58025	*Urocyon cinenreoargenteus*	Mandible
1095	LACMHC 58036	*Urocyon cinenreoargenteus*	Mandible
1096	LACMHC 68940	*Urocyon cinenreoargenteus*	Mandible
1097	W-9255	*Urocyon cinenreoargenteus*	Mandible
1098	W-9257	*Urocyon cinenreoargenteus*	Mandible
1099	W-9262	*Urocyon cinenreoargenteus*	Mandible
1100	W-9264	*Urocyon cinenreoargenteus*	Mandible
1101	W-9265	*Urocyon cinenreoargenteus*	Mandible
1102	W-9266	*Urocyon cinenreoargenteus*	Mandible
1103	W-9269	*Urocyon cinenreoargenteus*	Mandible
1104	W-9275	*Urocyon cinenreoargenteus*	Mandible
1105	W-9276	*Urocyon cinenreoargenteus*	Mandible
1106	W-9277	*Urocyon cinenreoargenteus*	Mandible
1107	W-9278	*Urocyon cinenreoargenteus*	Mandible
1108	W-9314	*Urocyon cinenreoargenteus*	Mandible
1090	LACMHC 58012	*Urocyon cinenreoargenteus*	C1
1091	LACMHC 58013	*Urocyon cinenreoargenteus*	C1
1092	LACMHC 58014	*Urocyon cinenreoargenteus*	C1
1109	LACMHC 57956	*Urocyon cinenreoargenteus*	Maxila
1110	LACMHC 57958	*Urocyon cinenreoargenteus*	Maxila
1111	LACMHC 58008	*Urocyon cinenreoargenteus*	Maxila
1112	W-9301	*Urocyon cinenreoargenteus*	Maxila
1113	C-297	*Urocyon cinenreoargenteus*	Skull
1114	HC-201	*Urocyon cinenreoargenteus*	Skull
1115	LACMHC 58016	*Urocyon cinenreoargenteus*	P4
1117	R-37488	*Urocyon cinenreoargenteus*	3rd Phalanx Mc III*
1118	LACMHC 58136	*Urocyon cinenreoargenteus*	3rd Phalanx Mt III*
1119	LACMHC 58104	*Urocyon cinenreoargenteus*	Astragalus
1120	R-35063	*Urocyon cinenreoargenteus*	Astragalus
1121	W-9014	*Urocyon cinenreoargenteus*	Astragalus
1122	W-9015	*Urocyon cinenreoargenteus*	Astragalus
1123	W-9016	*Urocyon cinenreoargenteus*	Astragalus
1124	W-9017	*Urocyon cinenreoargenteus*	Astragalus
1125	W-9018	*Urocyon cinenreoargenteus*	Astragalus
1126	W-9019	*Urocyon cinenreoargenteus*	Astragalus
1127	W-8798	*Urocyon cinenreoargenteus*	Femur
1128	W-8799	*Urocyon cinenreoargenteus*	Femur
1129	W-8815	*Urocyon cinenreoargenteus*	Femur
1130	W-8817	*Urocyon cinenreoargenteus*	Femur

Supplementary data 5.1. *Continued*

Number	Specimen Ref.	Species	Anatomical Element
1131	W-8818	*Urocyon cinenreoargenteus*	Femur
1132	W-8820	*Urocyon cinenreoargenteus*	Femur
1133	W-8822/8834	*Urocyon cinenreoargenteus*	Femur
1134	W-8824	*Urocyon cinenreoargenteus*	Femur
1135	W-8825	*Urocyon cinenreoargenteus*	Femur
1136	W-8826	*Urocyon cinenreoargenteus*	Femur
1137	LACMHC 58115	*Urocyon cinenreoargenteus*	Mt IV
1138	R-11308	*Urocyon cinenreoargenteus*	Mt IV
1139	W-8927	*Urocyon cinenreoargenteus*	Mt IV
1140	W-8933	*Urocyon cinenreoargenteus*	Mt IV
1141	W-8935	*Urocyon cinenreoargenteus*	Mt IV
1142	W-8936	*Urocyon cinenreoargenteus*	Mt IV
1143	W-8939	*Urocyon cinenreoargenteus*	Mt IV
1144	W-8940	*Urocyon cinenreoargenteus*	Mt IV
1145	W-8941	*Urocyon cinenreoargenteus*	Mt IV
1146	W-8945	*Urocyon cinenreoargenteus*	Mt IV
1147	LACMHC 58123	*Urocyon cinenreoargenteus*	1st Phalanx
1148	LACMHC 58125	*Urocyon cinenreoargenteus*	1st Phalanx
1149	R-47775	*Urocyon cinenreoargenteus*	1st Phalanx
1150	R-49237	*Urocyon cinenreoargenteus*	1st Phalanx
1151	W-9022	*Urocyon cinenreoargenteus*	1st Phalanx
1152	W-9026	*Urocyon cinenreoargenteus*	1st Phalanx
1153	W-9027	*Urocyon cinenreoargenteus*	1st Phalanx
1154	W-9028	*Urocyon cinenreoargenteus*	1st Phalanx
1155	W-9029	*Urocyon cinenreoargenteus*	1st Phalanx
1156	W-9036	*Urocyon cinenreoargenteus*	1st Phalanx
1157	R-36121	*Urocyon cinenreoargenteus*	Mc III
1158	W-9068	*Urocyon cinenreoargenteus*	Mc III
1159	W-9071	*Urocyon cinenreoargenteus*	Mc III
1160	W-9073	*Urocyon cinenreoargenteus*	Mc III
1161	W-9077	*Urocyon cinenreoargenteus*	Mc III
1162	W-9083	*Urocyon cinenreoargenteus*	Mc III
1163	W-9084	*Urocyon cinenreoargenteus*	Mc III
1164	W-9085	*Urocyon cinenreoargenteus*	Mc III
1165	W-9086	*Urocyon cinenreoargenteus*	Mc III
1166	W-9087	*Urocyon cinenreoargenteus*	Mc III
1167	W-8684	*Urocyon cinenreoargenteus*	Ulna
1168	W-8687	*Urocyon cinenreoargenteus*	Ulna
1169	W-8688	*Urocyon cinenreoargenteus*	Ulna
1170	W-8692	*Urocyon cinenreoargenteus*	Ulna
1171	W-8702	*Urocyon cinenreoargenteus*	Ulna
1172	W-8703	*Urocyon cinenreoargenteus*	Ulna

Supplementary data 5.1. *Continued*

Number	Specimen Ref.	Species	Anatomical Element
1173	LACMHC 58057	*Urocyon cinenreoargenteus*	Humerus
1174	W-8631	*Urocyon cinenreoargenteus*	Humerus
1175	W-8634	*Urocyon cinenreoargenteus*	Humerus
1176	W-8635	*Urocyon cinenreoargenteus*	Humerus
1177	W-8652	*Urocyon cinenreoargenteus*	Humerus
1178	W-8658	*Urocyon cinenreoargenteus*	Humerus
1179	W-8660	*Urocyon cinenreoargenteus*	Humerus
1180	W-8662	*Urocyon cinenreoargenteus*	Humerus
1181	W-8663	*Urocyon cinenreoargenteus*	Humerus
1182	W-8665	*Urocyon cinenreoargenteus*	Humerus
1183	W-8668	*Urocyon cinenreoargenteus*	Humerus
1184	W-8841	*Urocyon cinenreoargenteus*	Tibia
1185	W-8866	*Urocyon cinenreoargenteus*	Tibia
1186	W-8867	*Urocyon cinenreoargenteus*	Tibia
1187	W-8869	*Urocyon cinenreoargenteus*	Tibia
1188	W-8870	*Urocyon cinenreoargenteus*	Tibia
1189	W-8873	*Urocyon cinenreoargenteus*	Tibia
1190	W-8874	*Urocyon cinenreoargenteus*	Tibia
1191	W-8875	*Urocyon cinenreoargenteus*	Tibia
1192	W-8876	*Urocyon cinenreoargenteus*	Tibia
1193	W-8901	*Urocyon cinenreoargenteus*	Tibia
1194	LACMHC 82	*Ursus americanus*	Mandible
1195	LACMHC 82	*Ursus americanus*	Skull
1196	LACMHC 57906	*Ursus americanus*	m3
1197	LACMHC 57912	*Ursus americanus*	Mt IV
1198	LACMHC 57913	*Ursus americanus*	3rd Phalanx
1199	LACMHC 11928	*Ursus arctos*	C1
1200	HC 288	*Ursus arctos*	Mandible
1201	LACMHC 11928	*Ursus arctos*	Mandible
1202	LACMHC 57915	*Ursus arctos*	Mandible
1203	LACMHC 57917	*Ursus arctos*	m3
1205	LACMHC 57945	*Ursus arctos*	3rd Phalanx Mc III*
1208	LACMHC 57946	*Ursus arctos*	3rd Phalanx Mt III*
1209	HC 138728	*Ursus arctos*	Astragalus
1212	LACMHC A-1503	*Ursus arctos*	Femur
1214	T-2072	*Ursus arctos*	Mt IV
1216	LACMHC 57942	*Ursus arctos*	1st Phalanx
1218	LACMHC 57929	*Ursus arctos*	Mc III
1220	LACMHC 57926	*Ursus arctos*	Ulna

Supplementary data 5.2. *Classification of the ecological behaviour of all extant terrestrial carnivore mammals, and its affiliation to a particular functional subgroup and, subsequently, to a major functional group. The predictive power of the discriminant models for the functional groups and subgroups classifications are included at the end of the table.*

Species	Body size (g)	Body Size Category	Feeding Habits	Locomotor Behaviour	CFG	CFG (SubGr.)
Cuon alpinus	12760	Medium predator	Hipercarnivore	Cursorial	1	1
Lycaon pictus	22050.1	Large predator	Hipercarnivore	Cursorial	1	1
Canis lupus	39875	Large predator	Hipercarnivore	Cursorial	1	1
Acinonyx jubatus	50000	Mega-predator	Hipercarnivore	Cursorial	1	1
Panthera leo	161499.1	Mega-predator	Hipercarnivore	Cursorial	1	1
Crocuta crocuta	62999.9	Mega-predator	Meat/bone	Cursorial	1	1
Spilogale pygmaea	235.0	Micro-predator	Insectivore	Ambulatory	2	2
Galerella ochracea	550.0	Micro-predator	Insectivore	Ambulatory	2	2
Galerella sanguinea	550.0	Micro-predator	Insectivore	Ambulatory	2	2
Mungotictis decemlineata	650.0	Micro-predator	Insectivore	Ambulatory	2	2
Salanoia concolor	650.0	Micro-predator	Insectivore	Ambulatory	2	2
Galerella flavescens	750.0	Micro-predator	Insectivore	Ambulatory	2	2
Galerella pulverulenta	797.0	Micro-predator	Insectivore	Ambulatory	2	2
Mephitis macroura	801.3	Micro-predator	Insectivore	Ambulatory	2	2
Vulpes cana	1000	Small predator	Insectivore	Ambulatory	2	2
Fossa fossana	1500	Small predator	Insectivore	Ambulatory	2	2
Bdeogale crassicauda	1550	Small predator	Insectivore	Ambulatory	2	2
Paracynictis selousi	1640	Small predator	Insectivore	Ambulatory	2	2
Diplogale hosei	2000	Small predator	Insectivore	Ambulatory	2	2
Hemigalus derbyanus	2000	Small predator	Insectivore	Ambulatory	2	2
Bdeogale jacksoni	2500	Small predator	Insectivore	Ambulatory	2	2
Bdeogale nigripes	2500	Small predator	Insectivore	Ambulatory	2	2
Procyon pygmaeus	2500	Small predator	Insectivore	Ambulatory	2	2
Rhynchogale melleri	2500	Small predator	Insectivore	Ambulatory	2	2
Eupleres goudotii	3000	Small predator	Insectivore	Ambulatory	2	2
Chrotogale owstoni	3250	Small predator	Insectivore	Ambulatory	2	2
Ichneumia albicauda	3500	Small predator	Insectivore	Ambulatory	2	2
Helogale hirtula	289.0	Micro-predator	Insectivore	Fossorial	2	3
Helogale parvula	300.0	Micro-predator	Insectivore	Fossorial	2	3
Conepatus humboldtii	328.0	Micro-predator	Insectivore	Fossorial	2	3
Dologale dybowskii	350.0	Micro-predator	Insectivore	Fossorial	2	3
Crossarchus ansorgei	700.0	Micro-predator	Insectivore	Fossorial	2	3
Suricata suricatta	725.5	Micro-predator	Insectivore	Fossorial	2	3
Crossarchus platycephalus	1000	Small predator	Insectivore	Fossorial	2	3
Conepatus semistriatus	1200	Small predator	Insectivore	Fossorial	2	3
Crossarchus obscurus	1250	Small predator	Insectivore	Fossorial	2	3
Crossarchus alexandri	1500	Small predator	Insectivore	Fossorial	2	3
Mungos gambianus	1500	Small predator	Insectivore	Fossorial	2	3
Melogale personata	1702.5	Small predator	Insectivore	Fossorial	2	3

Supplementary data 5.2. *Continued*

Species	Body size (g)	Body Size Category	Feeding Habits	Locomotor Behaviour	CFG	CFG (SubGr.)
Mungos mungo	1925	Small predator	Insectivore	Fossorial	2	3
Mydaus javanensis	2500	Small predator	Insectivore	Fossorial	2	3
Mydaus marchei	2500	Small predator	Insectivore	Fossorial	2	3
Conepatus leuconotus	3500	Small predator	Insectivore	Fossorial	2	3
Proteles cristata	10000	Medium predator	Insectivore	Fossorial	2	3
Neovison vison	945.0	Micro-predator	Carnivore	Aquatic	3	4
Hydrictis maculicollis	4000	Medium predator	Carnivore	Aquatic	3	4
Pteronura brasiliensis	23999.9	Large predator	Carnivore	Aquatic	3	4
Poiana richardsonii	500.0	Micro-predator	Carnivore	Arboreal	4	5
Bassariscus sumichrasti	900.0	Micro-predator	Carnivore	Arboreal	4	5
Arctogalidia trivirgata	2250	Small predator	Carnivore	Arboreal	4	5
Genetta cristata	2500	Small predator	Carnivore	Arboreal	4	5
Prionodon pardicolor	512.0	Micro-predator	Carnivore	Scansorial	4	6
Genetta servalina	1055	Small predator	Carnivore	Scansorial	4	6
Genetta thierryi	1400	Small predator	Carnivore	Scansorial	4	6
Genetta abyssinica	1650	Small predator	Carnivore	Scansorial	4	6
Genetta angolensis	1650	Small predator	Carnivore	Scansorial	4	6
Genetta bourloni	1750	Small predator	Carnivore	Scansorial	4	6
Genetta genetta	1800	Small predator	Carnivore	Scansorial	4	6
Martes gwatkinsii	2043	Small predator	Carnivore	Scansorial	4	6
Genetta johnstoni	2225	Small predator	Carnivore	Scansorial	4	6
Genetta maculata	2225	Small predator	Carnivore	Scansorial	4	6
Genetta tigrina	2225	Small predator	Carnivore	Scansorial	4	6
Genetta poensis	2250	Small predator	Carnivore	Scansorial	4	6
Genetta victoriae	3000	Small predator	Carnivore	Scansorial	4	6
Genetta pardina	3100	Small predator	Carnivore	Scansorial	4	6
Eira barbara	3910	Small predator	Carnivore	Scansorial	4	6
Macrogalidia musschenbroekii	4000	Medium predator	Carnivore	Scansorial	4	6
Mustela itatsi	395.0	Micro-predator	Carnivore	Ambulatory	4	7
Galidictis fasciata	550.0	Micro-predator	Carnivore	Ambulatory	4	7
Herpestes javanicus	750.0	Micro-predator	Carnivore	Ambulatory	4	7
Galidia elegans	800.0	Micro-predator	Carnivore	Ambulatory	4	7
Galictis cuja	1000	Small predator	Carnivore	Ambulatory	4	7
Vulpes zerda	1100	Small predator	Carnivore	Ambulatory	4	7
Herpestes edwardsii	1324.2	Small predator	Carnivore	Ambulatory	4	7
Galidictis grandidieri	1400	Small predator	Carnivore	Ambulatory	4	7
Martes foina	1540.8	Small predator	Carnivore	Ambulatory	4	7
Herpestes smithii	1861.4	Small predator	Carnivore	Ambulatory	4	7
Herpestes urva	1863.2	Small predator	Carnivore	Ambulatory	4	7
Urocyon littoralis	1896	Small predator	Carnivore	Ambulatory	4	7
Vulpes macrotis	1900	Small predator	Carnivore	Ambulatory	4	7
Herpestes brachyurus	2000	Small predator	Carnivore	Ambulatory	4	7

Supplementary data 5.2. *Continued*

Species	Body size (g)	Body Size Category	Feeding Habits	Locomotor Behaviour	CFG	CFG (SubGr.)
Vulpes velox	2197.5	Small predator	Carnivore	Ambulatory	4	7
Herpestes semitorquatus	2371.1	Small predator	Carnivore	Ambulatory	4	7
Vulpes corsac	2400	Small predator	Carnivore	Ambulatory	4	7
Martes flavigula	2500	Small predator	Carnivore	Ambulatory	4	7
Herpestes fuscus	2700	Small predator	Carnivore	Ambulatory	4	7
Vulpes bengalensis	2726	Small predator	Carnivore	Ambulatory	4	7
Vulpes chama	2955	Small predator	Carnivore	Ambulatory	4	7
Viverricula indica	2980	Small predator	Carnivore	Ambulatory	4	7
Herpestes vitticollis	2994.7	Small predator	Carnivore	Ambulatory	4	7
Herpestes naso	3000	Small predator	Carnivore	Ambulatory	4	7
Galictis vittata	3200	Small predator	Carnivore	Ambulatory	4	7
Vulpes rueppellii	3250	Small predator	Carnivore	Ambulatory	4	7
Urocyon cinereoargenteus	3833.7	Small predator	Carnivore	Ambulatory	4	7
Lycalopex sechurae	4000	Medium predator	Carnivore	Ambulatory	4	7
Lycalopex gymnocercus	4690	Medium predator	Carnivore	Ambulatory	4	7
Herpestes ichneumon	5175	Medium predator	Carnivore	Ambulatory	4	7
Cerdocyon thous	5240	Medium predator	Carnivore	Ambulatory	4	7
Lycalopex vetulus	5350	Medium predator	Carnivore	Ambulatory	4	7
Vulpes vulpes	5488.3	Medium predator	Carnivore	Ambulatory	4	7
Atelocynus microtis	7750	Medium predator	Carnivore	Ambulatory	4	7
Lycalopex griseus	8280	Medium predator	Carnivore	Ambulatory	4	7
Canis mesomelas	8500	Medium predator	Carnivore	Ambulatory	4	7
Viverra zibetha	9000	Medium predator	Carnivore	Ambulatory	4	7
Viverra megaspila	9250	Medium predator	Carnivore	Ambulatory	4	7
Viverra civettina	9416.7	Medium predator	Carnivore	Ambulatory	4	7
Lycalopex culpaeus	9832.4	Medium predator	Carnivore	Ambulatory	4	7
Viverra tangalunga	10000	Medium predator	Carnivore	Ambulatory	4	7
Canis aureus	11479.1	Medium predator	Carnivore	Ambulatory	4	7
Civettictis civetta	12000	Medium predator	Carnivore	Ambulatory	4	7
Canis latrans	13406.3	Medium predator	Carnivore	Ambulatory	4	7
Gulo gulo	17012.6	Large predator	Carnivore	Ambulatory	4	7
Chrysocyon brachyurus	23249.8	Large predator	Carnivore	Ambulatory	4	7
Canis adustus	10249.9	Medium predator	Carnivore	Cursorial	4	8
Ictonyx striatus	1300	Small predator	Carnivore	Fossorial	4	8
Ictonyx libyca	2062.5	Small predator	Carnivore	Fossorial	4	8
Taxidea taxus	7107.6	Medium predator	Carnivore	Fossorial	4	8
Mellivora capensis	8500	Medium predator	Carnivore	Fossorial	4	8
Hyaena brunnea	32200.3	Large predator	Meat/bone	Ambulatory	5	9
Hyaena hyaena	41705.1	Large predator	Meat/bone	Ambulatory	5	9
Mustela lutreola	440.0	Micro-predator	Hipercarnivore	Aquatic	6	10
Neovison macrodon	945.0	Micro-predator	Hipercarnivore	Aquatic	6	10
Mustela subpalmata	87.5	Micro-predator	Hipercarnivore	Ambulatory	7	11

Supplementary data 5.2. *Continued*

Species	Body size (g)	Body Size Category	Feeding Habits	Locomotor Behaviour	CFG	CFG (SubGr.)
Mustela nivalis	103.9	Micro-predator	Hipercarnivore	Ambulatory	7	11
Mustela erminea	119.4	Micro-predator	Hipercarnivore	Ambulatory	7	11
Mustela frenata	147.0	Micro-predator	Hipercarnivore	Ambulatory	7	11
Mustela altaica	171.0	Micro-predator	Hipercarnivore	Ambulatory	7	11
Mustela kathiah	208.1	Micro-predator	Hipercarnivore	Ambulatory	7	11
Mustela felipei	211.3	Micro-predator	Hipercarnivore	Ambulatory	7	11
Lyncodon patagonicus	225.0	Micro-predator	Hipercarnivore	Ambulatory	7	11
Poecilogale albinucha	340.0	Micro-predator	Hipercarnivore	Ambulatory	7	11
Mustela sibirica	405.0	Micro-predator	Hipercarnivore	Ambulatory	7	11
Mustela nudipes	500.0	Micro-predator	Hipercarnivore	Ambulatory	7	11
Mustela strigidorsa	507.3	Micro-predator	Hipercarnivore	Ambulatory	7	11
Mustela africana	537.0	Micro-predator	Hipercarnivore	Ambulatory	7	11
Vormela peregusna	543.0	Micro-predator	Hipercarnivore	Ambulatory	7	11
Mustela lutreolina	706.6	Micro-predator	Hipercarnivore	Ambulatory	7	11
Mustela nigripes	850.0	Micro-predator	Hipercarnivore	Ambulatory	7	11
Mustela putorius	915.4	Micro-predator	Hipercarnivore	Ambulatory	7	11
Martes zibellina	1130	Small predator	Hipercarnivore	Ambulatory	7	11
Felis nigripes	1300	Small predator	Hipercarnivore	Ambulatory	7	11
Mustela eversmannii	1350	Small predator	Hipercarnivore	Ambulatory	7	11
Prionailurus rubiginosus	1350	Small predator	Hipercarnivore	Ambulatory	7	11
Catopuma badia	2500	Small predator	Hipercarnivore	Ambulatory	7	11
Felis margarita	2525	Small predator	Hipercarnivore	Ambulatory	7	11
Vulpes pallida	2800	Small predator	Hipercarnivore	Ambulatory	7	11
Genetta piscivora	3000	Small predator	Hipercarnivore	Ambulatory	7	11
Felis manul	3500	Small predator	Hipercarnivore	Ambulatory	7	11
Leopardus geoffroyi	3590	Small predator	Hipercarnivore	Ambulatory	7	11
Leopardus braccatus	3935	Small predator	Hipercarnivore	Ambulatory	7	11
Leopardus colocolo	3935	Small predator	Hipercarnivore	Ambulatory	7	11
Leopardus pajeros	3935	Small predator	Hipercarnivore	Ambulatory	7	11
Martes pennanti	4000	Medium predator	Hipercarnivore	Ambulatory	7	11
Vulpes lagopus	4867.6	Medium predator	Hipercarnivore	Ambulatory	7	11
Vulpes ferrilata	5000	Medium predator	Hipercarnivore	Ambulatory	7	11
Felis bieti	5500	Medium predator	Hipercarnivore	Ambulatory	7	11
Felis catus	5525	Medium predator	Hipercarnivore	Ambulatory	7	11
Felis silvestris	5525	Medium predator	Hipercarnivore	Ambulatory	7	11
Speothos venaticus	6000	Medium predator	Hipercarnivore	Ambulatory	7	11
Prionailurus planiceps	6750	Medium predator	Hipercarnivore	Ambulatory	7	11
Felis chaus	7003.4	Medium predator	Hipercarnivore	Ambulatory	7	11
Puma yagouaroundi	7874.9	Medium predator	Hipercarnivore	Ambulatory	7	11
Lynx rufus	8904.1	Medium predator	Hipercarnivore	Ambulatory	7	11
Leopardus jacobitus	9170	Medium predator	Hipercarnivore	Ambulatory	7	11
Lynx canadensis	9373.2	Medium predator	Hipercarnivore	Ambulatory	7	11

Supplementary data 5.2. *Continued*

Species	Body size (g)	Body Size Category	Feeding Habits	Locomotor Behaviour	CFG	CFG (SubGr.)
Lynx pardinus	9400	Medium predator	Hipercarnivore	Ambulatory	7	11
Canis simensis	10000	Medium predator	Hipercarnivore	Ambulatory	7	11
Prionailurus viverrinus	10850	Medium predator	Hipercarnivore	Ambulatory	7	11
Catopuma temminckii	11500	Medium predator	Hipercarnivore	Ambulatory	7	11
Leptailurus serval	12000	Medium predator	Hipercarnivore	Ambulatory	7	11
Caracal caracal	13749.9	Medium predator	Hipercarnivore	Ambulatory	7	11
Lynx lynx	17950	Large predator	Hipercarnivore	Ambulatory	7	11
Dusicyon australis	38888.3	Large predator	Hipercarnivore	Ambulatory	7	11
Uncia uncia	44167	Large predator	Hipercarnivore	Ambulatory	7	11
Puma concolor	51600	Mega-predator	Hipercarnivore	Ambulatory	7	11
Panthera onca	100000	Mega-predator	Hipercarnivore	Ambulatory	7	11
Panthera tigris	162564	Mega-predator	Hipercarnivore	Ambulatory	7	11
Ursus maritimus	388750.4	Mega-predator	Hipercarnivore	Ambulatory	7	11
Prionodon linsang	700.0	Micro-predator	Hipercarnivore	Scansorial	8	12
Martes americana	1250	Small predator	Hipercarnivore	Scansorial	8	12
Martes martes	1300	Small predator	Hipercarnivore	Scansorial	8	12
Leopardus guigna	2230	Small predator	Hipercarnivore	Scansorial	8	12
Leopardus tigrinus	2250	Small predator	Hipercarnivore	Scansorial	8	12
Leopardus wiedii	3250	Small predator	Hipercarnivore	Scansorial	8	12
Pardofelis marmorata	3250	Small predator	Hipercarnivore	Scansorial	8	12
Prionailurus bengalensis	3300	Small predator	Hipercarnivore	Scansorial	8	12
Prionailurus iriomotensis	3300	Small predator	Hipercarnivore	Scansorial	8	12
Cryptoprocta ferox	9500	Medium predator	Hipercarnivore	Scansorial	8	12
Profelis aurata	10650	Medium predator	Hipercarnivore	Scansorial	8	12
Leopardus pardalis	11900.1	Medium predator	Hipercarnivore	Scansorial	8	12
Neofelis nebulosa	19500	Large predator	Hipercarnivore	Scansorial	8	12
Panthera pardus	50249.8	Mega-predator	Hipercarnivore	Scansorial	8	12
Nasua nasua	3793.8	Small predator	Insectivore	Scansorial	8	13
Nasua narica	4030	Medium predator	Insectivore	Scansorial	8	13
Bassariscus astutus	1129.5	Small predator	Omnivore	Scansorial	9	14
Nandinia binotata	2000	Small predator	Omnivore	Scansorial	9	14
Paradoxurus jerdoni	2780.8	Small predator	Omnivore	Scansorial	9	14
Paradoxurus zeylonensis	2780.8	Small predator	Omnivore	Scansorial	9	14
Paradoxurus hermaphroditus	3200	Small predator	Omnivore	Scansorial	9	14
Paguma larvata	4300	Medium predator	Omnivore	Scansorial	9	14
Ailurus fulgens	4900	Medium predator	Omnivore	Scansorial	9	14
Helarctos malayanus	46000	Mega-predator	Omnivore	Scansorial	9	14
Ursus thibetanus	77500	Mega-predator	Omnivore	Scansorial	9	14
Tremarctos ornatus	140000.6	Mega-predator	Omnivore	Scansorial	9	14
Melogale moschata	938.5	Micro-predator	Omnivore	Fossorial	10	15
Melogale everetti	1547	Small predator	Omnivore	Fossorial	10	15
Conepatus chinga	1917.5	Small predator	Omnivore	Fossorial	10	15

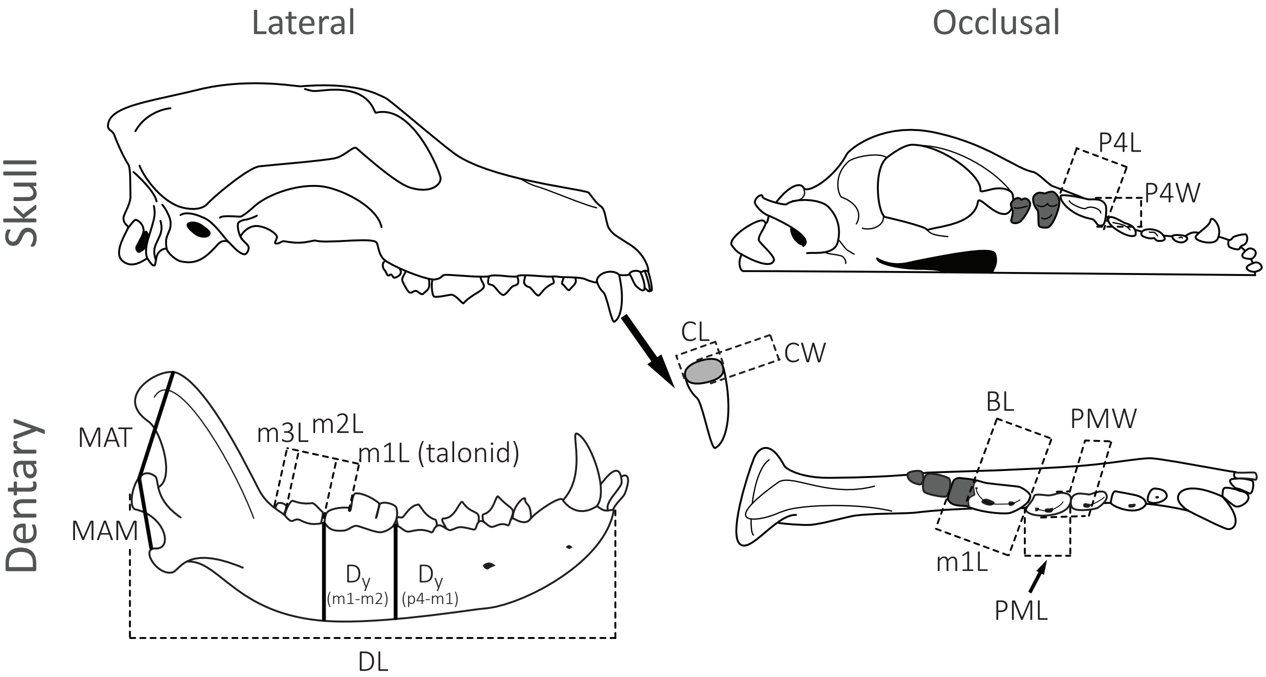
Supplementary data 5.2. *Continued*

Species	Body size (g)	Body Size Category	Feeding Habits	Locomotor Behaviour	CFG	CFG (SubGr.)
Melogale orientalis	2000	Small predator	Omnivore	Fossorial	10	15
Meles leucurus	6250	Medium predator	Omnivore	Fossorial	10	15
Arctonyx collaris	6356	Medium predator	Omnivore	Fossorial	10	15
Meles anakuma	11500	Medium predator	Omnivore	Fossorial	10	15
Meles meles	13000	Medium predator	Omnivore	Fossorial	10	15
Melursus ursinus	100000	Mega-predator	Omnivore	Fossorial	10	15
Poiana leightoni	600.0	Micro-predator	Omnivore	Arboreal	10	16
Bassaricyon lasius	1200	Small predator	Omnivore	Arboreal	10	16
Bassaricyon pauli	1200	Small predator	Omnivore	Arboreal	10	16
Bassaricyon alleni	1235	Small predator	Omnivore	Arboreal	10	16
Bassaricyon beddardi	1235	Small predator	Omnivore	Arboreal	10	16
Bassaricyon gabbii	1250	Small predator	Omnivore	Arboreal	10	16
Potos flavus	3000	Small predator	Omnivore	Arboreal	10	16
Arctictis binturong	13000	Medium predator	Omnivore	Arboreal	10	16
Aonyx cinerea	3990.4	Small predator	Omnivore	Aquatic	10	17
Cynogale bennettii	4500	Medium predator	Omnivore	Aquatic	10	17
Lutra sumatrana	5500	Medium predator	Omnivore	Aquatic	10	17
Lontra longicaudis	6555	Medium predator	Omnivore	Aquatic	10	17
Lontra provocax	7500	Medium predator	Omnivore	Aquatic	10	17
Lontra canadensis	8087.4	Medium predator	Omnivore	Aquatic	10	17
Lutrogale perspicillata	9000	Medium predator	Omnivore	Aquatic	10	17
Lutra lutra	10999.9	Medium predator	Omnivore	Aquatic	10	17
Lutra nippon	10999.9	Medium predator	Omnivore	Aquatic	10	17
Aonyx capensis	18999.8	Large predator	Omnivore	Aquatic	10	17
Enhydra lutris	23500	Large predator	Omnivore	Aquatic	10	17
Lontra felina	30600	Large predator	Omnivore	Aquatic	10	17
Spilogale putorius	341.0	Micro-predator	Omnivore	Ambulatory	11	18
Spilogale angustifrons	386.5	Micro-predator	Omnivore	Ambulatory	11	18
Spilogale gracilis	626.0	Micro-predator	Omnivore	Ambulatory	11	18
Cynictis penicillata	836.0	Micro-predator	Omnivore	Ambulatory	11	18
Martes melampus	1000	Small predator	Omnivore	Ambulatory	11	18
Nasuella olivacea	1340	Small predator	Omnivore	Ambulatory	11	18
Mephitis mephitis	2085	Small predator	Omnivore	Ambulatory	11	18
Liberiictis kuhni	2150	Small predator	Omnivore	Ambulatory	11	18
Lycalopex fulvipes	2250	Small predator	Omnivore	Ambulatory	11	18
Atilax paludinosus	3300	Small predator	Omnivore	Ambulatory	11	18
Nyctereutes procyonoides	4040	Medium predator	Omnivore	Ambulatory	11	18
Otocyon megalotis	4150	Medium predator	Omnivore	Ambulatory	11	18
Procyon lotor	5525	Medium predator	Omnivore	Ambulatory	11	18
Procyon cancrivorus	6949.9	Medium predator	Omnivore	Ambulatory	11	18
Ursus americanus	99949.4	Mega-predator	Omnivore	Ambulatory	11	18
Ailuropoda melanoleuca	108400	Mega-predator	Omnivore	Ambulatory	11	18

Supplementary data 5.2. *Continued*

Species	Body size (g)	Body Size Category	Feeding Habits	Locomotor Behaviour	CFG	CFG (SubGr.)
Ursus arctos	172720.4	Mega-predator	Omnivore	Ambulatory	11	18
Correctly extant classified species by DFA (%)					**77.2**	**99.2**

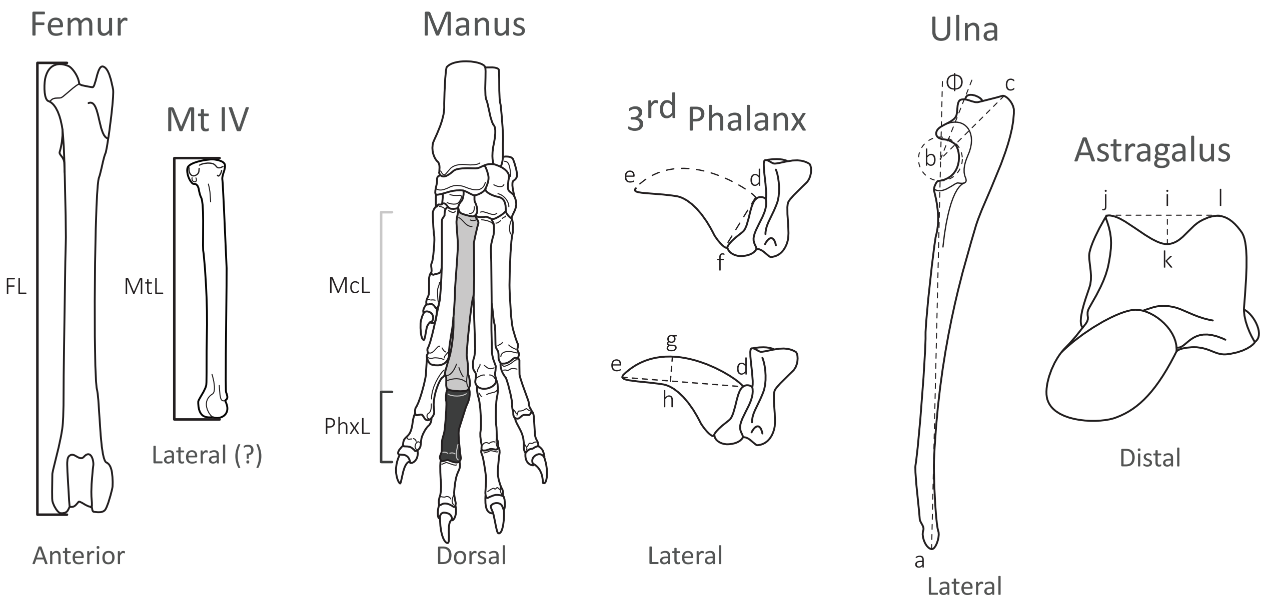
Supplementary figure 5.1. *Scheme of the measurements taken on the specimens to obtain the ratios used to infer the diet of the species from La Brea Tar Pits, for small (from Friscia et al. 2006) and large carnivores (from Van Valkenburgh 1988, 1989).*



Supplementary data 5.3. *List of measurements and ratios descriptions, together with the equations, used to infer the diet of the species from La Brea Tar Pits, for small (from Friscia et al. 2006) and large carnivores (from Van Valkenburgh 1988, 1989).*

Large Predators	CS	Upper Canine Shape	CW / CL	CW = Mediolateral width at the dentine-enamel junction.
				CL = Anteroposterior length at the dentine-enamel junction.
	PMD	Premolar Shape	PMW / PML	PMW = Maximum mediolateral width of the largest lower premolar (p4).
				PML = Maximum anteroposterior length of the largest lower premolar (p4).
	RPS	Premolar Size	$PMW / (BS)^{1/3}$	PMW = Maximum mediolateral width of the largest lower premolar (p4).
				BS = Body size (weight).
	RBL	Relative Blade Length	BL / m1L	BL = Anteroposterior length of the trigonid of the first lower molar (carnassial).
				m1L = Maximum length of the first lower molar (carnassial).
	RLGA	Relative Lower Gridding Area	$(TGA)^{1/2}/ BL$	TGA = Total gridding area of the lower molars: m1 talonid + m2 + m3 (if present). Area = maximum width*maximum length
				BL = As in RBL.
Small Predators	C1	Upper canine relative size	$(AC1)^{1/2}/ (Am1)^{1/2}$	CA = Area of the upper canine at the enamel junction (CL*CW).
				Am1 = Size of the lower first molar (lower carnassial). Size ≈ Area = W*L
	P4S	Premolar shape	PMW / PML	PMW = Maximum width of p4.
				PML = Maximum length of p4.
	P4Z	Relative length p4	PML / DL	PML = As in P4S
				DL = Dentary length.
	P4P	Relative size of the P4 protocone	P4W / P4L	P4W = Maximum width of P4.
				P4L = Maximum length of P4.
	PMZ	Relative total length of the premolars	p2L+p3L+p4L / DL	p2L = Maximum length of the p2
				p3L = Maximum length of the p3
				p4L = PML = As in P4S
				DL = As in P4Z
	RBL	Relative blade length	BL / m1L	BL = Anteroposterior length of the trigonid of the first lower molar (lower carnassial).
				m1L = Maximum length of the first lower molar (lower carnassial).
	M1BS	m1 blade size	BL / DL	BL = As in RBL
				DL = As in P4Z
	RLGA	Relative lower gridding area	$(LTGA)^{1/2} / BL$	LTGA = Total gridding area of the lower molars: m1 talonid + m2 (if present). Area = maximum width*maximum length
				BL = As in RBL.
	RUGA	Relative upper gridding area	$(UTGA)^{1/2} / P4L$	UTGA = Total gridding area of the upper molars: M1 + M2 (if present). Area = maximum width*maximum length
				P4L = Anteroposterior length of P4 (upper carnassial)
	M2S	m2 size relative to the dentary	$(m2A)^{1/2} / DL$	m2A = m2 area, measured as in RLGA. If no m2 was present, m2A was recorded as zero (and M2S = 0)
				DL = As in P4Z
	UM21	M2 size relative M1 size	$(M2A)^{1/2} / (M1A)^{1/2}$	M2A = M2 area, measured as in RUGA. If no m2 was present, M2A was recorded as zero (and UM21 = 0)
				M1A = M1 area, measured as in RUGA.
	MAT	Mechanical advantage of the temporalis muscle	MAT / DL	MAT = Distance from the mandibular condyle to the apex of the coronoid process.
				DL = As in P4Z
	MAM	Mechanical advantage of the masseter muscle	MAM / DL	MAM = Distance from the mandibular condyle to the ventral border of the mandibular angle.
				DL = As in P4Z
	IXP4	Second moment of area of the dentary at p4-m1 gap	$(I_x)^{1/4} / DL$	I_x = Moment of area of the dentary at the interdental gap between the p4 and the m1. $I_x = [(\pi*D_x)*(D_y)^3]/64$, where D_x and D_y are the maximum dentary width and height (depth) at the p3-p4 interdental gap.
				DL = As in P4Z
	IXM2	Resistance of the dentary to bending	$(I_x)^{1/4} / DL$	I_x = Moment of area of the dentary at the interdental gap between m1 and m2 (or posterior to the m1 if no m2 was present). I_x measured as in IXP4, but taken at the m1-m2 interdental gap (or posterior to the m1 if no m2 is present).
				DL = As in P4Z

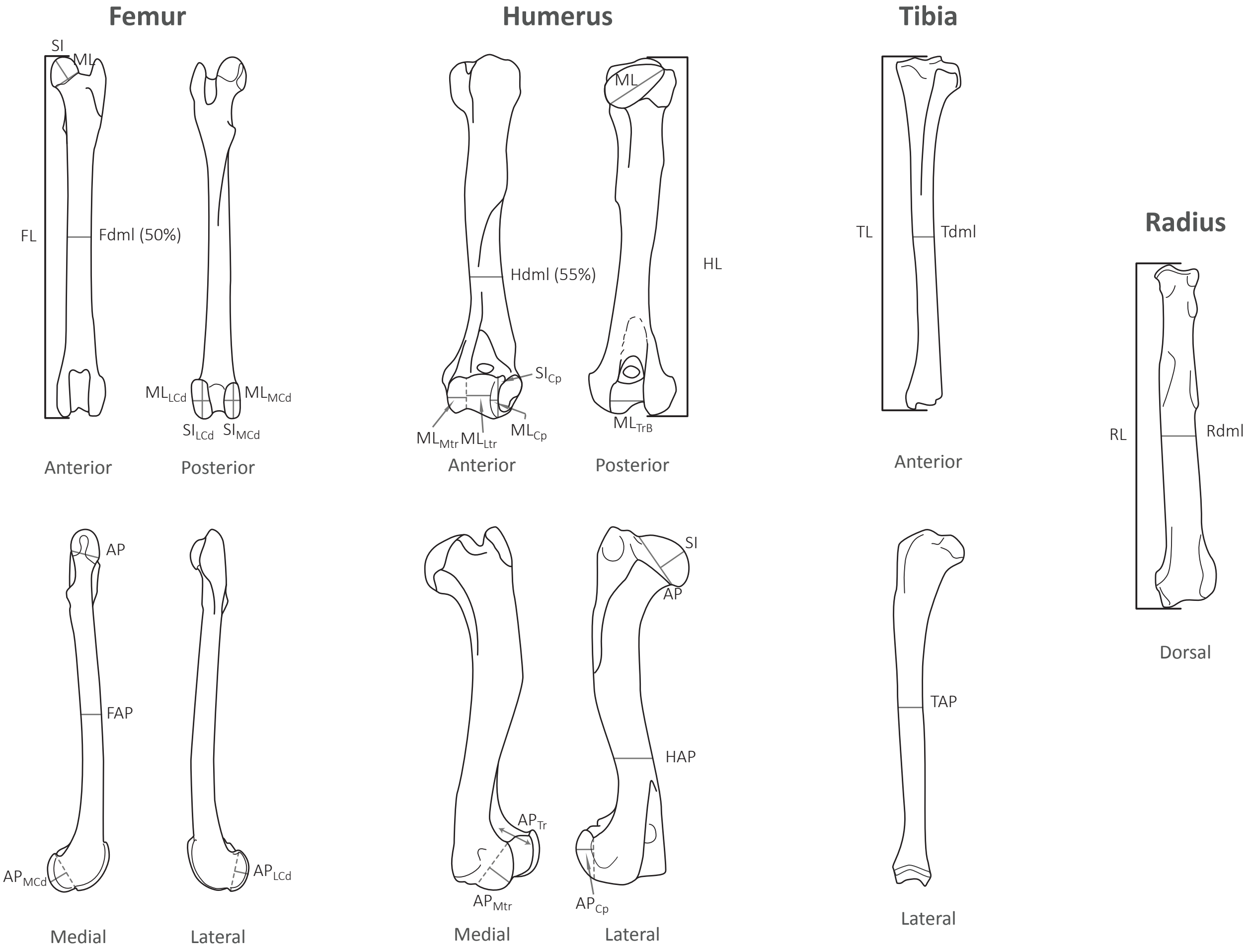
Supplementary figure 5.2. *Measurements taken on the specimens to obtain the ratios used to infer the locomotion of the species from La Brea Tar Pits (from Van Valkenburgh 1985, 1987).*



Supplementary data 5.4. *List of measurements and ratios descriptions, together with the equations, used to infer the locomotion of the species from La Brea Tar Pits (from Van Valkenburgh 1985, 1987).*

FMT	Hindlimb proportions	FL / MtL	FL = Maximum length of the femur.
			MtL = Maximum length of the fourth metatarsal.
MCP	Manus proportions	McL / PhxL	McL = Maximum length of the third metacarpal.
			PhxL = Maximum length of the proximal phalanx of the third digit.
OLL	Olecranon length	bc / ab	bc = Length of the olecranon process.
			ab = Length of the ulnar shaft.
OLA	Olecranon orientation	Φ	Anterior-posterior orientation of the olecranon process with respect to the ulnar shaft.
UD	Ungual phalanx depth	de(arc) / df	de(arc) = Length of the dorsal arc.
			df = Depth at ungual base.
ARCH	Ungual phx. dorsal arc	gh / de	gh = Maximum arc height
			de = Chord length (of the dorsal arc)
ASD	Astragalar trochlea depth	ik / jl	ik = Groove depth of the trocheal
			ji = Trochlea width

Supplementary figure 5.3. *Measurements taken on the specimens in order to obtain the mean body size of the species from La Brea Tar Pits, for felids (from Van Valkenburgh 1990), ursids (from Figueirido et al. 2010) and for the rest of carnivores (from Egi 2001).*



Supplementary data 5.5. *Description of the measurements and equations used to obtain the mean body size of the species from La Brea Tar Pits for felids (from Van Valkenburgh 1990), ursids (from Figueirido et al. 2010) and for the rest of carnivores (from Egi 2001). For felids and ursids both, Van Valkenburgh (1990) and Figueirido et al. (2010) used linear measurements in order to obtain the body size. Egi (2001), on the other hand, used both, linear measurements and articular dimensions (volume and surface area) of the bones. These articular dimensions were obtained by modelling the joints as geometric shapes (see supplementary data 5.6).*

Felids	First lower molar	m1L	Lower first molar length (as in diet)	Log B.S. = [3.05*Log(m1L)]-2.15	-
Ursids	Femur	FTL	Femur total length	Log B.S. = [2.37*Log(FL)]-3.85	-
		Fdml	Femur least mediolateral width of the diaphyseal shaft	Log B.S. = [2.63*Log(Fdml)]-1.71	-
	Humerus	HTL	Humerus total length	Log B.S. = [2.77*Log(HL)]-4.68	-
		Hdml	Humerus least mediolateral width of the diaphyseal shaft	Log B.S. = [2.60*Log(Hdml)]-1.65	-
	Tibia	TTL	Tibia total length	Log B.S. = [2.40*Log(TL)]-3.62	-
		Tdml	Tibia least mediolateral width of the diaphyseal shaft	Log B.S. = [2.33*Log(Tdml)]-0.96	-
	Radius	RTL	Radius total length	Log B.S. = [2.68*Log(RL)]-4.29	-
		Rdml	Radius least mediolateral width of the diaphyseal shaft	Log B.S. = [2.03*Log(Rdml)]-0.65	-
Other Carnivores	Femur	FL	Femur total length	Ln B.S. = [2.774*Ln(FL)]-11.43	1.01
		FTA	Femur subperiosteal area	Ln B.S. = [1.454*Ln(FTA)]-4.172	1.01
		FVprox	Femur proximal articular dimension (Volume)	Ln B.S. = [1.010*Ln(FVprox)]-4.748	1.00
		FSAprox	Femur proximal articular dimension (Area)	Ln B.S. = [1.522*Ln(FSAprox)]-6.848	1.00
		FVdist	Femur distal articular dimension (Volume)	Ln B.S. = [0.991*Ln(FVdist)]-4.264	1.01
		FSAdist	Femur distal articular dimension (Area)	Ln B.S. = [1.483*Ln(FSAdist)]-6.295	1.01
	Humerus	HL	Humerus total length	Ln B.S. = [2.642*Ln(HL)]-10.52	0.99
		HTA	Humerus subperiosteal area	Ln B.S. = [1.366*Ln(HTA)]-3.789	1.01
		HVprox	Humerus proximal articular dimension (Volume)	Ln B.S. = [0.987*Ln(HVprox)]-4.816	1.01
		HSAprox	Humerus proximal articular dimension (Area)	Ln B.S. = [1.476*Ln(HSAprox)]-6.989	1.02
		HVdist	Humerus distal articular dimension (Volume)	Ln B.S. = [0.913*Ln(HVdist)]-4.049	0.99
		HSAdist	Humerus distal articular dimension (Area)	Ln B.S. = [1.376*Ln(HSAdist)]-6.196	0.98
	Tibia	TL	Tibia total length	Ln B.S. = [2.694*Ln(TL)]-10.97	0.98
		TTA	Tibia subperiosteal area	Ln B.S. = [1.312*Ln(TTA)]-3.417	1.01

Supplementary data 5.6. *Resume of equivalence between the articular joint and the geometric shape used by Egi (2001), together with the formulae used to calculate the articular dimensions, in order to obtain the area and volume of the articular joints. These articular dimensions are then used to calculate the mean body size of the carnivore species from La Brea Tar Pits using the equations from Egi (2001) (see supplementary data 5.5).*

Geometric shape	Bone	Measurement	Equation
Oval	Femur, Humerus, Tibia	Area (TA)	$TA = \pi/4*(x*y)$
Partial Sphere	Femur (prox.), Humerus (prox.)	Volume (V)	$V = \pi/3*d^2*(3r-d)$
		Area (A)	$A = 2\pi*d*r$
Elliptical Cylinder (Half)	Femur (condyles), Humerus (capitulum)	Volume (V)	$V = \pi/2*(a*b*w)$
		Area (A)	$A = \pi*w*[(a^2+b^2)/2]^{1/2}$
Cylinder (Half)	Humerus (posterior trochlea)	Volume (V)	$V = \pi/2*(c^2*w)$
		Area (A)	$A = \pi*c*w$
Partial Cone (Half)	Humerus (anterior trochlea, lesser and major)	Volume (V)	$V = \pi/6*L*[R^2+r^2+(R*r)]$
		Area (A)	$A = \pi/2*[(R+r)*(L^2+[R-r]^2)^{1/2}]$

Bone	Bone part	Ep. Term	Bone measurement
Femur	Diaphysis	x	FML (= Fdml)
		y	FAP
	Proximal	d	ML
		r	(SI+AP)/4
	Distal	2a	SI_{LCd}; SI_{MCd}
		2b	AP_{LCd}; AP_{MCd}
		w	ML_{LCd}; ML_{MCd}
Humerus	Diaphysis	x	HML(≈ Hdml)
		y	HAP
	Proximal	d	SI
		r	$(SI/2)+([(ML+AP)/2]^2/[8*SI])$
	Distal (Capitulum)	2a	SI_{Cp}
		2b	AP_{Cp}
		w	ML_{Cp}
	Troclea (posterior)	2c	AP_{Tr}
		w	ML_{TrB}
	Troclea (anterior)	L	ML_{MTr}; ML_{LTr}
		R	AP_{MTr}; AP_{Cp}
		2r	AP_{Tr} (both)
Tibia	Diaphysis	x	TML (= Tdml)
		y	TAP

Supplementary data 5.7. *Resume of the equivalence between the articular joint measurements and the equations terms for the different measured bone (see supplementary data 5.6), in order to obtain the mean body size of the carnivore species from La Brea Tar Pits.*

Supplementary data 5.8. *Carnivore functional spectra of the 26 modern localities from the North America used in this research. N. corresponds to the number in map from figure 5.1. Cl. denotes the climate biome. S. is the number of carnivore species from every locality.*

N	Locality	S	Cl	Carnivore Functional Groups (CFG)										
				1	2	3	4	5	6	7	8	9	10	11
1	Río Verde	18	II/III	5.56	11.11	0	22.22	0	0	27.78	11.11	5.56	0	16.67
2	Santiago	9	II/III	0	0	0	44.44	0	0	22.22	0	11.11	0	22.22
3	El Paso	13	III	0	7.69	0	30.77	0	0	23.08	7.69	7.69	0	23.08
4	Phoenix	17	III	5.88	11.76	0	23.53	0	0	17.65	5.88	5.88	5.88	23.53
5	Fresno	15	IV	0	0	6.67	33.33	0	0	20	0	6.67	6.67	26.67
6	San Diego	10	IV	0	0	0	30	0	0	30	0	10	0	30
7	Jacksonville	9	V	0	0	11.11	33.33	0	0	22.22	0	0	11.11	22.22
8	New Orleans	12	V	8.33	0	8.33	16.67	0	0	33.33	0	0	8.33	25
9	Cleveland	18	VI	5.56	0	5.56	27.78	0	0	33.33	5.56	0	5.56	16.67
10	Colorado Springs	13	VI	0	0	0	30.77	0	0	30.77	7.69	7.69	0	23.08
11	Prince Rupert	11	VI	9.09	0	9.09	9.09	0	0	36.36	9.09	0	9.09	18.18
12	St Louis	10	VI	0	0	10	30	0	0	20	0	0	10	30
13	Medicine Lake	9	VII	0	0	11.11	33.33	0	0	33.33	0	0	0	22.22
14	Rapid City	19	VII	5.26	0	5.26	26.32	0	0	31.58	0	0	5.26	26.32
15	Santa Fé	14	VII	0	0	0	35.71	0	0	28.57	0	7.14	0	28.57
16	Winnemucca	10	VII	0	0	0	20	0	0	40	0	0	10	30
17	Edmonton	13	VIII	7.69	0	7.69	23.08	0	0	38.46	0	0	0	23.08
18	Fairbanks	12	VIII	8.33	0	8.33	25	0	0	25	8.33	0	8.33	16.67
19	Fort Smiith	16	VIII	6.25	0	6.25	18.75	0	0	37.50	6.25	0	6.25	18.75
20	Gaspé	12	VIII	0	0	8.33	8.33	0	8.33	33.33	8.33	0	8.33	25
21	Smookey Falls	13	VIII	7.69	0	7.69	15.38	0	0	38.46	7.69	0	7.69	15.38
22	Baker Lake	6	IX	16.67	0	0	33.33	0	0	50	0	0	0	0
23	Barrow	10	IX	10	0	10	30	0	0	50	0	0	0	0
24	Cape Hope Advances	8	IX	12.50	0	0	25	0	0	50	0	0	12.50	0
25	Cooper Mine	9	IX	11.11	0	0	33.33	0	0	44.44	0	0	0	11.11
26	Port Harrison	9	IX	11.11	0	0	22.22	0	0	55.56	0	0	11.11	0

6. CONCLUSIONES.

Conclusiones principales

En esta tesis hemos abordado el estudio de la estructura de las comunidades de mamíferos mediante la aplicación de diversas metodologías de inferencia paleoambiental, tanto clásicas como de nueva creación. Además, el incluir una perspectiva temporal nos ha permitido analizar si la estructura de las comunidades es estable en el tiempo o si, por el contrario, ha cambiado bajo la influencia de los grandes eventos de cambio climático acaecidos en la Tierra.

Esta combinación de técnicas clásicas y nuevas responde a las limitaciones de los estudios de inferencia paleoecológica y paleoambiental clásicos, válidos sólo para las asociaciones de mamíferos más comunes. Por ejemplo, en los casos en los que el registro muestra una inversión en la proporción de herbívoros frente a carnívoros ha sido necesario desarrollar una nueva metodología, "grupos funcionales de carnívoros", que nos permite realizar inferencias con los datos disponibles. Para ello, no sólo hemos comprobado la utilidad de esta nueva metodología como herramienta descriptiva de la estructura de las comunidades de carnívoros terrestres, sino que también hemos analizado la influencia de los diferentes climas terrestres sobre esta estructura. Por último, una vez comprobada su utilidad, hemos aplicado esta nueva metodología sobre la fauna de carnívoros del conjunto de yacimientos fósiles de Rancho la Brea, comprobando cómo las glaciaciones del Pleistoceno y el calentamiento Holoceno estructuraron la comunidad de predadores del suroeste de Norteamérica.

Dado que cada uno de los objetivos de la presente tesis se pueden desarrollar de forma independiente, hemos considerado oportuno presentar por separado las conclusiones principales para cada capítulo.

Estudio de las relaciones predador-presa, en las comunidades de mamíferos, a partir del estudio de su distribución de tamaños corporales (Capítulo 2)

En este apartado analizamos la utilidad de los cenogramas como herramienta para describir la estructura de las comunidades de mamíferos terrestres. Para ello tratamos de determinar las relaciones que se establecen entre los dos grupos tróficos, predadores y presas, de dichas comunidades a través del estudio de su distribución de tamaños corporales.

Pese a que nuestros resultados permitieron establecer una relación entre el desarrollo de un salto en la distribución de tamaños corporales de las presas, en torno a las tallas medias, y el tamaño medio de los predadores, la magnitud de dicho salto está fuertemente condicionada por las condiciones climáticas del medio en el que habitan las especies de dicha comunidad, particularmente aquellas relacionadas con la temperatura. Además, los resultados de nuestros análisis no mostraron relación alguna entre la aparición del salto en la distribución de tamaños corporales de las presas y el desarrollo de otro salto en la distribución de tamaños de los predadores. Por el contrario, observamos que el factor que condiciona la continuidad en la distribución de tamaños corporales de los predadores es la aridez del medio, al menos en las regiones tropicales del planeta.

Por tanto, debemos rechazar la hipótesis inicial propuesta por Valverde, en la que planteaba la posibilidad de que las distribuciones de tamaños corporales de ambos grupos tróficos, predadores y presas, estaban condicionadas por relaciones de tipo evolutivo, como consecuencia de una carrera de armamentos establecida entre ambos gremios. Por el contrario, vemos que son las condiciones del medio en el que habitan las especies, particularmente la temperatura y la aridez, los factores que determinan la distribución de tamaños corporales de las comunidades de mamíferos. Estas conclusiones apoyan los resultados de trabajos previos en los que se apuntaba la utilidad de esta metodología como herramienta de inferencia ambiental.

Inferencias paleoambientales a partir del estudio de las estructura de tamaños corporales de las faunas de mamíferos del Aragoniense medio de la cuenca de Madrid (Capítulo 3)

El estudio de seis faunas de mamíferos del Mioceno medio de la Cuenca de Madrid, con edades comprendidas entre los 15,5 y lo 13,5 M.a., particularmente de sus presas, muestra una serie de cambios en su distribución de tamaños corporales durante el Aragoniense medio. Analizando la estructura de los cenogramas y el espectro de tamaños corporales de estas comunidades fósiles, observamos que los cambios detectados en las distribuciones de tamaños corporales de las diferentes comunidades reflejan eventos de cambio climático acaecidos durante ese periodo en la Península Ibérica. El enfriamiento global relacionado con el establecimiento de una masa de hielo permanente en la Antártida, hace aproximadamente 14 millones de años, provocó un cambio hacia condiciones más áridas y frías en la Cuenca de Madrid, quedando reflejado como cambios en la estructura de las comunidades de presas analizadas.

Los ambientes inferidos en nuestros análisis son todos tropicales y semi-áridos.

Sin embargo, observamos unas fluctuaciones entre condiciones relativamente más áridas y otras más húmedas. Partiendo de unas condiciones áridas y abiertas al comienzo de la secuencia, detectamos un primer cambio hacia condiciones relativamente más húmedas y con una mayor cobertera forestal. Posteriormente, a mitad de la secuencia, y coincidiendo con el evento de enfriamiento global del Mioceno medio, se produjo un retorno hacia condiciones más abiertas y áridas. Por último, al final de la secuencia observamos como las condiciones se estabilizaron, volviendo a encontrarnos con un ambiente relativamente más húmedo y cerrado.

Estructura de las comunidades de carnívoros terrestres: descripción e influencia de los grandes eventos geográficos y climáticos (Capítulo 4)

En este capítulo desarrollamos una nueva metodología, denominada Grupos Funcionales de Carnívoros (o CFG en sus siglas en inglés), que nos permite describir la estructura de las comunidades de carnívoros terrestres actuales. Además, esta metodología posibilita también relacionar la estructura de la comunidad y el tipo de ambiente en el que esta habita, siendo de gran utilidad en los estudios de tipo paleoambiental en los que el registro fósil muestra un predominio de la fauna de carnívoros.

Esta metodología nos permitió clasificar las 250 especies de carnívoros terrestres (orden Carnivora) en 11 grupos funcionales diferentes, según sus características ecológicas (dieta, locomoción y tamaño corporal). Observamos que los factores ecológicos que determinan principalmente la agrupación de las especies en los distintos grupos funcionales son la dieta y el tipo de locomoción. La preponderancia de ambos factores sobre el tamaño corporal tiene que ver con el balance energético de las propias especies, estrechamente condicionado por ambas variables ecológicas.

Además, en este capítulo, mostramos como el espectro funcional de las comunidades de carnívoros terrestres discrimina tipos de biomas, siempre que se tenga en cuenta la historia biogeográfica de las faunas. La gran mayoría de las localidades analizadas presentan una estructura compleja acorde al tipo de bioma en el que se localizan. Tan sólo en unos pocos casos se observan distorsiones en la estructura la comunidad, derivadas del aislamiento geográfico, la influencia de biomas adyacentes, o los efectos de las glaciaciones del Pleistoceno.

No obstante, pese a su alta capacidad discriminante, también concluimos que no existe ningún grupo funcional que pueda diferenciar tipos de ambientes por si solo. En general, es la complejidad estructural de las comunidades y la interacción de los diferentes grupos funcionales lo que diferencia las comunidades de los distintos ambientes. Sin embargo, existen dos biomas en los que la estructura de las comunidades de carnívoros, al ser más homogénea, es visualmente diferenciable del resto. Se trata de las comunidades de tundra y pluvisilva, donde factores como las glaciaciones del Pleistoceno, en el caso de la tundra, o la alta tasa de diversidad ecológica, en el caso de la pluvisilva, homogeneizaron la estructura de sus comunidades a lo largo del tiempo y el espacio, lo que permite diferenciarlas del resto con mayor claridad.

Evolución del paisaje del suroeste de Norteamérica durante el Pleistoceno a partir del estudio de la estructura de las comunidades de carnívoros presentes en Rancho la Brea (Capítulo 5)

En este capítulo, una vez confirmada la utilidad de los grupos funcionales de carnívoros como descriptores de la estructura de las comunidades de predadores e indicadores ambientales, procedimos a aplicar esta metodología sobre la fauna de carnívoros presente el yacimiento de Rancho La Brea. El análisis de las comunidades de carnívoros presentes en varios de los pozos de brea localizados en el yacimiento nos permitió detectar dos grandes cambios ambientales que modificaron el paisaje del suroeste de Norteamérica en los últimos 30.000 años. Partiendo de unas condiciones de bosque o matorral mediterráneo asociado a la mayor aridez impuesta por las glaciaciones del Pleistoceno, el paisaje cambió gradualmente hasta establecerse una taiga, como consecuencia de la mayor humedad asociada al calentamiento del Holoceno. Estas condiciones se mantuvieron hasta que, asociada al aumento gradual de la temperatura, la aridez aumentó y la taiga fue nuevamente sustituida por el matorral mediterráneo que encontramos en Los Ángeles en la actualidad.

Pese a que la fauna presente en Rancho la Brea es muy similar a la que encontramos en Los Ángeles a día de hoy, estos cambios ambientales impusieron una serie de limitaciones, directa o indirectamente, sobre las especies que habitaban en la región durante el periodo estudiado, modificando estructuralmente de manera significativa las diferentes comunidades de carnívoros analizadas. Dichas modificaciones estructurales se limitaron a un escaso número de grupos funcionales, como consecuencia de la alternancia entre condiciones áridas-abiertas y húmedas-forestales o de procesos de tipo "*bottom-up*" (cascada trófica ascendente) asociados a la extinción de la megafauna de herbívoros del Pleistoceno, así como la competencia interespecífica establecida entre algunas especies.

Breve reflexión final

A tenor de los resultados obtenidos en esta tesis podemos puntualizar que las comunidades de mamíferos se pueden entender como entidades dinámicas integradas, cuyos componentes interactúan entre ellos y con el medio que los rodea, evolucionando con cada cambio. Pueden ser descompuestas en componentes de menor rango (gremios), en los que estas relaciones siguen presentes e incluso pueden mostrar características del ecosistema que pueden pasar desapercibidas al ser estudiadas en un rango jerárquico superior.

En este trabajo hemos ahondado en la capacidad del peso, variable ecológica de primer orden, como descriptor de la estructura de las comunidades de mamíferos a partir del estudio de los cenogramas. Pese a que el estudio de su estructura no nos ha permitido describir las relaciones tróficas que se establecen entre los diferentes miembros de las comunidades, sí nos ha permitido analizar la respuesta las comunidades de mamíferos ante los cambios ambientales como un todo, además de colocarnos en una posición ventajosa para inferir respuestas coordinadas por parte de grupos de especies ante una situación de cambio climático como la que vivimos en la actualidad. Por otro lado, particular relevancia tiene el trabajo llevado a cabo con las comunidades de carnívoros, que abre nuevas vías de investigación y desmantela ideas preconcebidas acerca de la independencia entre la estructura de las comunidades de carnívoros y el ambiente en el que estos habitan.

Saber qué rango de tamaños puede verse más afectado por un cambio drástico en el clima, qué factores ambientales condicionan en mayor medida a las comunidades o qué adaptaciones ecológicas resultan más útiles para responder ante las eventualidades climáticas, puede ayudarnos a centrar esfuerzos de conservación en aquellas especies susceptibles de verse más intensamente afectadas. Sin embargo, la estructuración de una comunidad no es un proceso instantáneo, por lo que se hace necesario incluir en nuestros estudios el factor tiempo, para analizar así cómo cambian las comunidades a lo largo de la historia. Dada su amplia representación en el registro fósil, el análisis de la estructura de las comunidades de mamíferos se descubre como una herramientas de gran utilidad en estudios de tipo paleoecológico y paleoambiental.

Por supuesto aún nos quedan muchas incógnitas por resolver, como cuál es el peso de las relaciones filogenéticas en las adaptaciones ecológicas de las especies, cómo influye la historia biogeográfica de las diferentes comunidades en sus patrones de estructuración o si podemos detectar un gradiente latitudinal en las tallas medias de las microcomunidades de mamíferos. Habrá pues quien piense que este trabajo está condicionado por la limitación en la información que maneja pero, parafraseando a Campoamor, "En este mundo traidor, nada es verdad ni mentira, todo es según el aumento del cristal con que se mira”. Miremos pues a través de las distintas lentes del objetivo.

7. APPENDIX 1.

Appendix 1. *Geographic data of the 100 modern localities used in the analysis. Mp corresponds to the number in the different maps from chapters 2 to 5. ^{a}Cl. Climate biome. R represents the realm where the locality is allocated (1) Nearctic realm; (2) Neotropical realm; (3) Palaearctic realm; (4) Afrotropic realm; (5) Indomalaysian realm. Note: All faunal distributions were reviewed following Wilson & Reeder (1993) and Wilson & Mittermeier (2009)*

Mp	^{a}Cl.	R	Locality	Country	Latitude	Longitude	Altitude	References	
								Fauna	Climate
1	II/III	1	Río Verde	Mexico	21° 56' N	99° 59' W	987 m	Hall 1981	Meteorological Office 1980
2	II/III	1	Santiago	Mexico	23° 28' N	109° 43' W	125 m	Hall 1981	Canty et al. 2008
3	III	1	El Paso	USA	31° 48' N	106° 24' W	1194 m	Hall 1981	Meteorological Office 1980
4	III	1	Phoenix	USA	33° 26' N	112° 01' W	340 m	Hall 1981	Court 1974
5	IV	1	Fresno	USA	36° 46' N	119° 42' W	100 m	Hall 1981	Court 1974
6	IV	1	San Diego	USA	32° 44' N	117° 10' W	4 m	Hall 1981, Smithsonian National Museum of Natural History 2006	Meteorological Office 1980
7	V	1	Jacksonville	USA	30° 25' N	81° 39' W	7 m	Hall 1981, Smithsonian National Museum of Natural History 2006	Meteorological Office 1980
8	V	1	New Orleans	USA	29° 57' N	90° 04' W	3 m	Hall 1981	Court 1974
9	VI	1	Cleveland	USA	41° 24' N	81° 51' W	237 m	Hall 1981	Court 1974
10	VI	1	Colorado Springs	USA	38° 49' N	104° 43' W	1882 m	Hall 1981	Meteorological Office 1980
11	VI	1	Prince Rupert	Canada	54° 17' N	136° 23' W	16 m	Hall 1981	Hare & Hay 1974
12	VI	1	St Louis	USA	38° 45' N	90° 23' W	163 m	Hall 1981, Smithsonian National Museum of Natural History 2006	Meteorological Office 1980
13	VII	1	Medicine Lake	USA	48° 29' N	104° 27' W	595 m	Hall 1981, Smithsonian National Museum of Natural History 2006	Meteorological Office 1980
14	VII	1	Rapid City	USA	44° 01' N	103° 03' W	965 m	Hall 1981	Court 1974
15	VII	1	Santa Fé	USA	35° 40' N	105° 55' W	2195 m	Smithsonian National Museum of Natural History 2006.	Meteorological Office 1980
16	VII	1	Winnemucca	USA	40° 54' N	117° 48' W	1434 m	Hall 1981	Meteorological Office 1980
17	VIII	1	Edmonton	Canada	53° 34' N	113° 31 W	676 m	Hall 1981, Smithsonian National Museum of Natural History 2006	Meteorological Office 1980
18	VIII	1	Fairbanks	USA	64° 49' N	147° 52' W	133 m	Hall 1981	Hare & Hay 1974
19	VIII	1	Fort Smith	Canada	60° 01' N	11° 58' W	62 m	Hall 1981	Hare & Hay 1974
20	VIII	1	Gaspé	Canada	48° 50' N	64° 29' W	28 m	Hall 1981, Smithsonian National Museum of Natural History 2006	Meteorological Office 1980

Mp	^{a} Cl.	R	Locality	Country	Latitude	Longitude	Altitude	References	
								Fauna	Climate
21	VIII	1	Smoky falls	Canada	46° 27' N	79° 55' W	227 m	Hall 1981, Smithsonian National Museum of Natural History 2006	Meteorological Office 1980
22	IX	1	Baker Lake	Canada	64° 18' N	96° 00' W	9 m	Hall 1981, Smithsonian National Museum of Natural History 2006	Meteorological Office 1980
23	IX	1	Barrow	USA	71° 18' N	156° 47' W	7 m	Hall 1981	Hare & Hay 1974
24	IX	1	Cape Hope Advances	Canada	61° 05' N	69° 33' W	73 m	Hall 1981, Smithsonian National Museum of Natural History 2006	Meteorological Office 1980
25	IX	1	Coppermine	Canada	67° 49' N	115° 05' W	9 m	Hall 1981, Smithsonian National Museum of Natural History 2006	Meteorological Office 1980
26	IX	1	Port Harrison	Canada	58° 27' N	78° 08' W	6 m	Hall 1981	Hare & Hay 1974
27	I	2	Paramaribo	Suriname	5° 51' N	55° 10' W	3 m	Eisenberg 1989	Snow 1976
28	I	2	Puerto Limón	Costa Rica	10° 00' N	083° 03' W	-3 m	Eisenberg 1989, Eisenberg & Redford 1999	Canty et al. 2008
29	I	2	Sao Paulo	Brazil	23° 37' S	46° 39' W	807 m	Eisenberg 1989, Eisenberg & Redford 1999	Rudloff 1981
30	I	2	Tumaco	Colombia	1° 49' N	78° 47' W	4 m	Eisenberg 1989	Snow 1976
31	I	2	Uapes	Brazil	0° 08' S	67° 05' W	83 m	Eisenberg 1989, Eisenberg & Redford 1999	Meteorological Office 1958
32	II	2	Acapulco	Mexico	16° 50' N	99° 56' W	3 m	Eisenberg 1989, Eisenberg & Redford 1999	Meteorological Office 1958
33	II	2	Brasilia	Brazil	15° 47' S	47° 56' W	1158 m	Eisenberg 1989, Eisenberg & Redford 1999	Mühr 2007
34	II	2	Puerto Ayacucho	Venezuela	5° 41' S	67° 38' W	99 m	Eisenberg 1989	Snow 1976
35	II	2	Roque Sáenz Peña	Argentina	26° 49' S	60° 27' W	92 m	Redford & Eisenberg 1992	Prohaska 1976
36	II/III	2	Catamarca	Argentina	28° 26' S	65° 46' W	547 m	Redford & Eisenberg 1992	Prohaska 1976
37	II/III	2	Las Piedras	Venezuela	11° 42' N	70° 12' W	15 m	Eisenberg 1989	Snow 1976
38	II/III	2	Remanso	Brasilia	9° 41' S	42° 04' W	411 m	Eisenberg 1989, Eisenberg & Redford 1999	Rudloff 1981
39	III	2	Arica	Chile	18° 28' S	70° 22' W	29 m	Redford & Eisenberg 1992	Miller 1976
40	III	2	Mendoza	Argentina	32° 53' S	68° 49' W	800 m	Eisenberg 1989, Eisenberg & Redford 1999	Meteorological Office 1958
41	IV	2	Santiago de Chile	Chile	33° 27' S	70° 42' W	520 m	Redford & Eisenberg 1992	Miller 1976
42	V	2	Corrientes	Argentina	27° 28' S	58° 49' W	60 m	Redford & Eisenberg 1992	Prohaska 1976
43	V	2	Montevideo	Uruguay	34° 52' S	56° 12' W	22 m	Redford & Eisenberg 1992	Meteorological Office 1958

Mp	[a] Cl.	R	Locality	Country	Latitude	Longitude	Altitude	References	
								Fauna	Climate
44	V	2	Puerto Montt	Chile	41° 28' S	72° 57' W	13 m	Redford & Eisenberg 1992	Miller 1976
45	VI	2	Evangelistas	Chile	52° 24' S	75° 06' W	55 m	Redford & Eisenberg 1992	Miller 1976
46	VII	2	Maquinchao	Argentina	41° 15' S	68° 43' W	888 m	Redford & Eisenberg 1992	Canty et al. 2008
47	VII	2	Puerto Sta. Cruz	Argentina	50° 01' S	68° 32' W	12 m	Redford & Eisenberg 1992	Prohaska 1976
48	III	3	Assuan	Egypt	23° 58' N	33° 40' E	194 m	Corbet 1978	Estienne & Godard 1970
49	III	3	Jacobabad	Pakistan	28° 17' N	68° 29' E	57 m	Corbet & Hill 1992	Meteorological Office 1966
50	III	3	Muscat	Oman	23° 37' N	58 35' E	4 m	Corbet 1978	Taha et al. 1981
51	III	3	Smara	Western Sahara	26° 44' N	11° 26' W	140 m	Corbet 1978	Font Tullot 1955
52	IV	3	Aleppo	Syria	36° 11' N	37° 13' E	395 m	Corbet 1978	Taha et al. 1981
53	IV	3	Isfahan	Iran	32° 37' N	51° 40' E	1598 m	Corbet 1978	Taha et al. 1981
54	IV	3	Potenza	Italy	40°38'N	15°46'E	823 m	Mitchell-Jones et al. 1999	Meteorological Office 1972
55	IV	3	Sanlúcar de Barrameda	Spain	36° 47' N	6° 21' W	30 m	Corbet 1978	Elías & Ruiz 1977
56	IV	3	Tripoli	Greece	37° 31' N	22° 21'E	661m m	Mitchell-Jones et al. 1999	Meteorological Office 1972
57	IV	3	Tunis	Tunisia	36° 50' N	10° 14' E	3 m	Corbet 1978	Meteorological Office 1983
58	V	3	Fuzhou	China	26° 05' N	119° 18' E	88 m	Corbet & Hill 1992	Watts 1969
59	V	3	Kagoshima	Japan	31° 34' N	130° 33' E	4 m	Corbet 1978	Arakawa & Taga 1969
60	V	3	Pingnan	China	23° 23' N	110° 03' E	39 m	Corbet & Hill 1992	Canty et al. 2008
61	V	3	Shaoguan	China	55° 45' N	37° 34' E	156 m	Corbet & Hill 1992	Canty et al. 2008
62	VI	3	Belgrade	Serbia	44° 48'N	20° 28'E	132 m	Mitchell-Jones et al. 1999	Meteorological Office 1972
63	VI	3	Blagoveshchensk	Russia	50° 15' N	106° 30' E	142 m	Corbet 1978	Meteorological Office 1966
64	VI	3	Moscow	Russia	55° 45' N	37° 34' E	156 m	Mitchell-Jones et al. 1999	Meteorological Office 1972
65	VI	3	Tsingtao	China	36° 04' N	120° 19' E	77 m	Corbet 1978	Watts 1969
66	VI	3	Vlissingen	Netherlands	51° 27' N	3° 36' E	12 m	Corbet 1978	Arléry 1970
67	VII	3	Almaty	Kazakhstan	43° 16' N	76° 53' E	775 m	Corbet 1978	Meteorological Office 1966
68	VII	3	Fort Shevchenko	Kazakhstan	44° 33' N	50° 17' E	23 m	Corbet 1978	Lydolph 1977
69	VII	3	Baotou	China	40° 34' N	109° 50' E	1044 m	Corbet 1978	Watts 1969

Mp	ª Cl.	R	Locality	Country	Latitude	Longitude	Altitude	References	
								Fauna	Climate
70	VII	3	Urumqi	China	43° 47' N	87° 37' E	912 m	Corbet 1978	Watts 1969
71	VIII	3	Erbogachen	Russia	61° 16' N	108°01' E	287 m	Corbet 1978	Lydolph 1977
72	VIII	3	Kajaani	Finland	64° 17' N	27° 41' E	134 m	Corbet 1978	Werner 1970
73	VIII	3	Nikolayevsk-on-Amur	Russia	53° 08' N	140° 45' E	21 m	Corbet 1978	Meteorological Office 1966
74	VIII	3	Petropavlovsk	Russia	52° 53' N	158° 42' E	87 m	Corbet 1978	Meteorological Office 1966
75	VIII	3	Serov	Russia	59° 36' N	60° 32' E	132 m	Corbet 1978	Lydolph 1977
76	IX	3	Bulum	Russia	70° 45' N	127° 47' E	35 m	Corbet 1978	Meteorological Office 1966
77	IX	3	Malye-Karmakuly	Russia	72° 23' N	55° 44' E	16 m	Corbet 1978	Lydolph 1977
78	IX	3	Mys Chelyuskin	Russia	77° 43' N	104° 17' E	6 m	Corbet 1978	Lydolph 1977
79	IX	3	Mys Shmidta	Russia	68° 55' N	179° 17' E	6 m	Corbet 1978	Lydolph 1977
80	IX	3	Nizhnekolymsk	Russia	68° 32' N	160° 59' E	5 m	Corbet 1978	Meteorological Office 1966
81	I	4	Greenville	Liberia	05° 04' N	09° 05' W	10 m	Kingdon 1971, 1979, 1982ab, 1997, Dorst & Dandelot 1973, Corbet 1978, Nowak 1999, Skinner & Chimimba 2005, World Wildlife Fund. 2006	Meteorological Office 1983
82	I	4	Kribi	Cameroon	2° 57' N	9° 54' E	624 m	Kingdon 1971, 1974ab, 1977, 1979, 1982ab, Nowak 1999, Dorst & Dandelot 1973	Bultot & Griffiths 1972
83	I	4	Yangambi	D. R. Congo	0° 49' N	24° 29' E	487 m	Kingdon 1971, 1974ab, 1977, 1979, 1982ab, Nowak 1999, Dorst & Dandelot 1973	Bultot & Griffiths 1972
84	II	4	Moundou	Chad	8° 37' N	16° 04' E	420 m	Kingdon 1971, 1974ab, 1977, 1979, 1982ab, Nowak 1999, Dorst & Dandelot 1973	Griffiths 1972a
85	II	4	Mtwara	Tanzania	10° 16' S	40° 16' E	113 m	Kingdon 1971, 1974, 1977, 1979, 1982ab	Griffiths 1972b
86	II	4	Ziguinchor	Senegal	12° 35' N	16° 16' W	10 m	Kingdon 1971, 1974ab, 1977, 1979, 1982ab, Nowak 1999, Dorst & Dandelot 1973	Griffiths 1972a
87	II/III	4	Gaborone	Botswana	24° 41' S	25° 55' E	983 m	Kingdon 1971, 1979, 1982ab, 1997, Dorst & Dandelot 1973, Corbet 1978, Nowak 1999, Skinner & Chimimba 2005	Meteorological Office 1983
88	II/III	4	Tulear	Madagascar	23° 23' S	43° 44' E	9 m	Garbutt 2007	Griffiths & Ranaivoson 1972
89	II/III	4	Voi	Kenya	3° 24' S	38° 34' E	560 m	Kingdon 1971, 1974ab, 1977, 1979, 1982ab	Griffiths 1972b

Mp	[a] Cl.	R	Locality	Country	Latitude	Longitude	Altitude	References	
								Fauna	Climate
90	II/III	4	Zinder	Niger	13° 48' N	8° 59' E	510 m	Kingdon 1971, 1974ab, 1977, 1979, 1982ab, Nowak 1999, Dorst & Dandelot 1973	Griffiths 1972a
91	III	4	Galcaio	Somalia	6° 46' N	47° 26' E	240 m	Kingdon 1971, 1979, 1982ab, 1997, Dorst & Dandelot 1973, Corbet 1978, Nowak 1999, Skinner & Chimimba 2005, World Wildlife Fund. 2006	Meteorological Office 1983
92	III	4	Lüderitz Bay	Namibia	26° 38' S	15° 06' E	23 m	Kingdon 1971, 1974ab, 1977, 1979, 1982ab, Nowak 1999, Dorst & Dandelot 1973	Schulze 1972
93	IV	4	Cape Town	South Africa	33° 54'S	18° 32' E	17 m	Skinner & Chimimba 2005	Schulze 1972
94	V	4	East London	South Africa	33° 02' S	27° 52' E	125 m	Skinner & Smithers 1990, Skinner & Chimimba 2005	Schulze 1972
95	I	5	Medan	Indonesia	3° 40' N	98° 35' E	14 m	Corbet & Hill 1992	Sukanto 1969
96	I	5	Silchar	India	24° 49' N	92° 48' E	29 m	Corbet & Hill 1992	Meteorological Office 1966
97	II	5	Patna	India	25° 37' N	85° 10' E	53 m	Corbet & Hill 1992	Rao 1981
98	II	5	Phnom Penh	Cambodia	11° 33' N	104° 55' E	12 m	Corbet & Hill 1992	Nieuwolt 1981
99	II	5	Trivandrum	India	8° 29' N	18° 32' E	64 m	Corbet & Hill 1992	Rao 1981
100	II/III	5	Jaipur	India	26° 49' N	75° 48' E	390 m	Corbet & Hill 1992	Rao 1981

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