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ORIGINAL ARTICLE

Body size, biomic specialization and range size of African large mammals

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ABSTRACT

Aim The goal of this paper is to examine the relationships between body size, biomic specialization and range size in the African large mammals, which are defined as all the African species corresponding to the orders Primates, Carnivora, Proboscidea, Perissodactyla, Hyracoidea, Tubulidentata, Artiodactyla and Pholidota.

Location The study used the large mammal assemblage from Africa.

Methods The degree of biomic specialization of African large mammals is investigated using the biomic specialization index (BSI) for each mammal species, based on the number of biomes it inhabits. Range size for each species is measured as the latitudinal extent of the geographical distribution of the species. We have analysed our data using both conventional cross-species analyses and phylogenetically independent contrasts.

Results There is a polygonal relationship between species biomic specialization and body size. While small and large species are biomic specialists, medium-sized species are distributed along the whole range of biomic specialization. The latitudinal extent–body size relationship is approximately triangular. Small-bodied species may have either large or small ranges, whereas large-bodied ones have only large ranges. A positive correlation between latitudinal extent and biomic specialization is evident, although their relationship is better described as triangular.

Main conclusions We found a polygonal relationship between species biomic specialization and body size, which agrees with previous arguments that small-bodied species have more limited dispersal and, therefore, they may come to occupy a lesser proportion of their potential inhabitable biomes. On the other hand, large-bodied species are constrained to inhabit biomes with a high productivity. A polygonal relationship between species latitudinal extent and body size in African large mammals agrees with previous studies of the relationship between range size and body size in other continents. The independent study of the macroecological pattern in biomic specialization highlights different factors that influence the body size–range size relationship. Although body size is usually implicated as a correlate of both specialization and geographical range size in large mammals, much of the variation in these variables cannot be attributed to size differences but to biome specific factors such as productivity, area, history, etc.

Keywords

Africa, bioclimatology, biogeography, biome, comparative analysis, ecological pattern, ecological specialization, macroecology, Mammalia.

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INTRODUCTION

Although frequently described simply as a positive correlation, the relationship between geographical range size, which is classically considered one of the measures of species rarity (Gaston, 1994), and body size at large scales is commonly rather more complex than this implies (Gaston & Blackburn, 1996b). Usually, species of all body sizes may have large geographical ranges. Nevertheless, the minimum range size exhibited by species tends to increase with body size. Thus, small species have a variety of range sizes, but large-bodied species have only large ranges. Several mechanisms have been proposed to explain this triangular relationship (see review in Gaston & Blackburn, 1996b; Reed, 2003). However, interactions of body size with numerous ecological variables often obscure the final picture, making it difficult to draw firm conclusions about the nature of these relationships. Summarizing, a triangular relationship between range size and body size means that body size cannot be used as a simple predictor of geographical range size.

A large number of other ecological traits have been postulated as correlates of the range sizes of species (Kunin & Gaston, 1996). Typically, ecological specialization has been proposed as one such correlated variable (Glazier, 1980; Brown, 1984; Pomeroy & Ssekabiira, 1990; Pagel *et al.*, 1991; Eeley & Foley, 1999; Harcourt, 2000; Harcourt *et al.*, 2002; Reed, 2003). In fact, the degree of ecological specialization features in both the macroecological and macroevolutionary research programmes. Several measures of specialization and generalization (or lesser vs. greater adaptability) have been proposed: number of habitat types occupied by a taxon, number of food types used and number of subtaxa per taxon (Pagel *et al.*, 1991; Eeley & Foley, 1999; Harcourt, 2000). Nevertheless, indices of this kind have several caveats. For example, rare taxa, precisely because they are rare, are likely to be less studied than are common taxa. This implies that there is less knowledge about species variation in behaviour and ecology for these rare taxa (Cotgreave & Pagel, 1997). If this is the case, information on rare taxa could be strongly biased (Doherty & Harcourt, 2004). Besides, some of these measures are difficult to apply to continent-wide, intercontinental and global comparisons as well as to highly dissimilar taxa. Therefore, it is necessary to use ecological categories of specialization that are sufficiently broad to solve these problems. In this paper, we single out biomic specialization as of particular relevance (following Vrba, 1987) and propose a measure of biomic specialization (or adaptability) that can be used at global scale and with disparate taxa (following Hernández Fernández, 2001). The degree of biomic specialization is defined as the degree to which one species is able to inhabit different biomes.

Previous macroecological studies have focused primarily on the interactions between abundance, latitude, geographical range size and body size (see references in Blackburn & Gaston, 1996; Gaston & Blackburn, 1999). As abundance measures are not available for most of the species studied in this paper and the latitudinal pattern in biomic specialization has been studied in a separate paper (Hernández Fernández & Vrba, 2005a), here we examine the large-scale relationships between biomic specialization and the last two of these variables (body size and range size) in the African large mammals, and their dependence on the macroecological and macroevolutionary mechanisms that shaped them.

In this paper we focus on the entire large mammal fauna of Africa. This assemblage has a number of features that make it particularly suitable for such an investigation. First, Africa is a relatively discrete landmass, nearly isolated from other land areas. As a result, a high proportion of its fauna (90% of the large mammals) is endemic to the continent. Problems resulting from the extension beyond the region of species geographical ranges are thus largely eliminated (Blackburn & Gaston, 1996, 1998). Secondly, the distributions of large mammals through most of Africa are well known (at least at the relevant resolution). This minimizes the potential for spurious relationships. Because distribution maps are available for all extant African large mammals, the potential for bias introduced by missing species is also minimized. This potential is not entirely eradicated, because some mammal species may as yet be undiscovered (Blackburn & Gaston, 1998); but, such species are expected to constitute a minimal proportion of the total. Thirdly, the high diversity of habitat tolerance in African large mammals permits the study of almost the complete range of possible mammal biome-ecotypes in a tropical–subtropical region. Fourthly, according to Wilson & Reeder (1993), the African large mammal fauna is the most speciose of any region of comparable size. Therefore, not only are the taxa well known, but they also offer a good sample size for detecting possible patterns. Finally, Africa has been less influenced than other continents by the Pleistocene megafaunal extinction (Kurtén, 1971; Martin & Klein, 1984; Owen-Smith, 1988; Lyons *et al.*, 2004) and hence, the analysis should reflect patterns based upon long-term evolutionary processes rather than historical species depletion.

METHODS

Assemblage

The study area is the African continent. It excludes Madagascar and all offshore islands. The data represent the global geographical distributions of all the 245 large land mammal species occurring within Africa. Here, we define large mammals as those included in a series of orders, which are characterized on average by medium–large body size (Primates, Carnivora, Proboscidea, Perissodactyla, Hyracoidea, Tubulidentata, Artiodactyla and Pholidota). It excludes Chiroptera, Insectivora, Lagomorpha, Macroscelidea and Rodentia. The list also contains species that became extinct in historical times. Species introduced by humans are omitted. We have followed the species-level taxonomy of Wilson & Reeder (1993).

Information on the geographical distributions of African mammal species was obtained from Dorst & Dandelot (1969), Kingdon (1971, 1977, 1979, 1982a,b), Skinner & Smithers (1990), Wilson & Reeder (1993) and Kingdon (1997). We have also used Corbet (1978), Hall (1981) and Corbet & Hill (1992) for species with geographical ranges falling outside Africa.

Data on biomic specialization

In order to characterize each mammal species bioclimatically, we use the climatic classification of Walter (1970), summarized in Table 1 and mapped in Allué Andrade (1990). This typology has been selected because it has a simple nomenclature and coincides with traditional biomes (Odum, 1971; Lacoste & Salanon, 1973; Lieth, 1975; Strahler & Strahler, 1987), termed zonobiomes by Walter (1970). Climatic zones I–V exist in Africa today. In this paper the terms biome, zonobiome and climate zone are used synonymously (Table 1) and henceforth we only use biome in order to facilitate comprehension. Additionally, vegetation belts in mountains must be taken into account. The latitudinal gradient represents a habitat series analogous to that of biomes in a latitudinal gradient (Walter, 1970; Walter & Breckle, 1986). We can recognize several vegetation belts in the sub-Saharan mountains (Walter & Breckle, 1986; Kingdon, 1997): lowlands belt, montane forest belt (analogous to biome V), subalpine forest-ericacean belt (analogous to biome VIII) and afroalpine belt (analogous to biome VII). In the Atlas mountains the recognized vegetation belts are (Walter, 1970; Walter & Breckle, 1991): lowlands belt, montane deciduous forest belt (analogous to biome VI), subalpine forest belt (analogous to biome VIII) and alpine belt (analogous to biome VII).

We applied the methodology developed by Hernández Fernández (2001) to the African large mammals: for each species we computed the biomic specialization index (BSI), which is the number of biomes inhabited by it (Hernández Fernández & Vrba, 2005a). Thus BSI equals 1 for most specialized species whereas for generalist species it could be as high as 10. This index can be used globally, allowing intercontinental comparisons, and is also valuable for comparison among very dissimilar taxa (Hernández Fernández & Vrba, in press). The decision on the number of biomes inhabited by a species was based on the following. If 15% or more of the geographical range of a species is situated within a biome, the species was recorded as present in that biome. As some climatic dominions, which were defined as a continuous terrestrial area within one biome only (Hernández Fernández, 2001), are small enough to comprise < 15% of the total distribution ranges of species with large range sizes, a species was also recorded as present in a specific biome if it inhabits 50% or more of one climatic dominion (Hernández Fernández, 2001). Hernández Fernández & Vrba (2005a) show the 13 climatic dominions determined for the African continent. The presence in a mountain vegetation belt was also recorded as presence in the corresponding analogous biome.

Table 1 Climatic typology used in this paper (modified from Walter, 1970) and its correspondence with world vegetation types (zonobiomes). Walter considers II/III as a zonoecotone between tropical forests and deserts, but we consider it as a zonobiome

	Climate zone	Zonobiome
I	Equatorial	Evergreen tropical rain forest
II	Tropical with summer rains	Tropical deciduous woodland
II/III	Transition tropical semiarid	Savanna
III	Subtropical arid	Subtropical desert
IV	Winter rain and summer drought	Sclerophyllous woodland-shrubland
V	Warm-temperate	Temperate evergreen forest
VI	Typical-temperate	Nemoral broadleaf-deciduous forest
VII	Arid-temperate	Steppe to cold desert
VIII	Cold-temperate (boreal)	Boreal coniferous forest (taiga)
IX	Arctic	Tundra

Data on body size and geographical range size

We collected information on body mass (g) for each African large mammal species using Kingdon (1997). We used the arithmetic mean of the limits for ranges of masses.

Following Stevens (1989), we use the latitudinal extent of the geographical range as a measure of geographical range size. This measure was calculated as the range in latitude degrees between the northernmost extant limit and the southernmost extant limit of the species geographical range.

Analyses

We have used $\log_{10}$ transformed body mass and latitudinal extent in all the analyses. This allows our results to be compared directly with previous interspecific analyses of these variables.

As closely related species are more likely to share similar ecological features because of a common ancestor, data for different species cannot be considered as independent points in comparative studies (Harvey & Mace, 1982; Felsenstein, 1985; Harvey & Pagel, 1991; Harvey *et al.*, 1995). There is, however, debate about the importance or usefulness of using phylogenetic corrections to control shared evolutionary history when performing comparative analyses (Rees, 1995; Westoby *et al.*, 1995a,b,c). It has also been suggested that cross taxa analyses can be as statistically valid and as biologically informative as independent contrasts (Ricklefs & Starck, 1996; Björklund, 1997; Price, 1997; Harvey & Rambaut, 1998, 2000; Losos, 1999). Therefore, we have analysed our data using both approaches. First, a cross-species analysis was made, where each species was treated as an independent data point, and the correlation between the relevant variables were calculated. Then, we performed phylogenetically independent contrasts ('contrasts' henceforward), for which we used the CAIC v.2.6.9 package (Purvis & Rambaut, 1995).

CAIC calculates the difference in the studied variables between pairs of species based on their phylogenetic proximity. This contrast represents the amount of evolutionary divergence since species speciated from their common ancestor. In addition, CAIC may calculate contrasts at internal nodes of the phylogeny. Because of the general lack of knowledge about the mode of character evolution in the considered variables, we have used two sets of contrasts. First, we have used nested contrasts ('crunch' command in CAIC). As the ancestral species at the nodes are not known, this method needs to estimate 'ancestral' states for each variable at each node in a phylogeny and, thus, it assumes a specific model of trait evolution to calculate expected contrast values between pairs of taxa at those nodes. Particularly, CAIC assumes Felsenstein's (1985) Brownian model of phenotypic evolution, in which continuous characters evolve as a stochastic process (Purvis & Rambaut, 1995; Martins & Hansen, 1996). Values at nodes are calculated as averages of the species or nodes that evolved from them. Nested contrasts are commonly preferred in comparative tests of correlated character evolution, because they maximize sample size and use all of the data (Harvey & Pagel, 1991). Nevertheless, they lose strict independence if the model adopted for character evolution is inadequate (Harvey & Purvis, 1991). Therefore, we have also analysed a set of non-nested contrasts between related pairs of taxa ('brunch' command in CAIC), which are independent under less stringent assumptions than a Brownian motion (Martins & Hansen, 1996). Results for both sets of contrasts are presented, and significance levels were only considered to be robust where they are in agreement. As branch lengths are not known between many nodes, we assigned all branches the same length, which implicitly assumes an essentially punctuational mode of evolution (Purvis & Rambaut, 1995).

Contrasts were analysed in two ways, as follows: (1) under the null hypothesis of no association, the contrasts will be positive in about half of the comparisons. A sign test (Arbuthnott, 1710) was used to asses the significance of departures from this null prediction; (2) as regression uses magnitudes of both variables, we used least-squares regression through the origin (Garland *et al.*, 1992) to test whether differences in one variable predicted the contrasts in the other.

The phylogenetic tree used to calculate contrasts was based on information gathered from supertrees for Carnivora (Bininda-Emonds *et al.*, 1999), Primates (Purvis, 1995; Purvis & Webster, 1999), Ruminantia (Hernández Fernández & Vrba, 2005b) and the families of Mammalia (Liu *et al.*, 2001). These supertrees combine information from a large number of molecular and morphological phylogenies. Additional phylogenetic information was collected for Pholidota, Hyracoidea, Perissodactyla and non-ruminant Artiodactyla (Roche, 1972; Churcher & Richardson, 1978; Cooke, 1978; Patterson, 1978; Eisenmann, 1979; Kaminski, 1979; Bennet, 1980; Harris & Porter, 1980; Lowenstein & Ryder, 1985; George & Ryder, 1986; Flint *et al.*, 1990; Nowak, 1991; Pickford, 1993; Wilson & Reeder, 1993; White, 1995; Rasmussen *et al.*, 1996; Oakenfull & Clegg, 1998; Gaudin & Wible, 1999). The phylogeny is shown in Appendix S1.

RESULTS

Relationship between biomic specialization and body size

The correlation between the BSI and body mass across species is not statistically significant ($r = 0.099$, $P = 0.123$, $n = 242$ species). In fact, a polygonal relationship appears to be a better description than a linear one (Fig. 1). The lower boundary of this polygon is well defined by the maximum possible biomic specialization (BSI = 1). The left and right boundaries suggest that only species with intermediate body mass (between 5 and 100 kg) can become biome generalists. These generalist taxa are varied; species with BSI equal to or larger than 6 are found in Primates, Hyracoidea, Proboscidea, Artiodactyla and Carnivora (Hernández Fernández & Vrba, in press).

Thus, across all species, African large mammals show a roughly polygonal relationship between biome specialization and body mass, with specialist species displaying almost all the ranges between small and large body masses, but generalist species tending to have only medium body mass (Fig. 1). In order to test statistically the form of the upper boundaries to this polygonal relationship we followed the procedure proposed by Blackburn *et al.* (1992). The data in Fig. 1 are divided into size classes of equal range, selecting for use in a regression those points with the highest BSI values in each size class. As

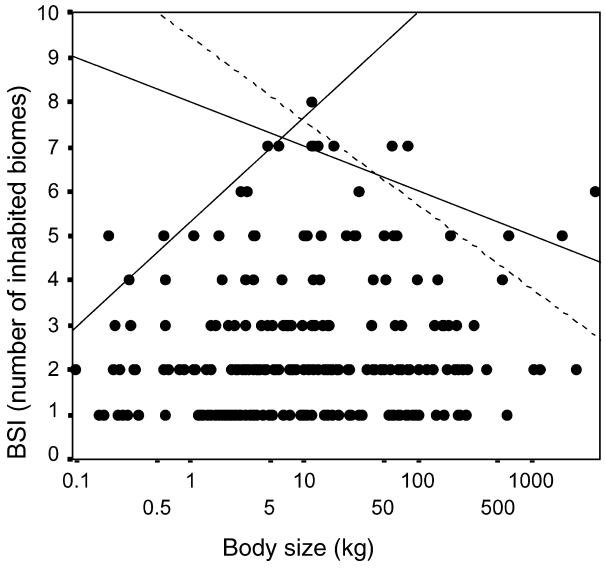

Figure 1 The relationship between biomic specialization (BSI; number of inhabited biomes) and body mass (kg) for the large mammals in Africa. Note the logarithmical scale for body mass. Regression lines corresponding to the analyses in Table 2 are shown (15 intervals of equal range of body size class). For the large-bodied species two lines, including (solid) and excluding (dashed) *Loxodonta*, are shown.

the value of the slope depends on the number of size classes selected, which is arbitrary, we computed this analysis several times, over a range of interval numbers from 6 to 15 (following the suggestion of Blackburn *et al.*, 1992). Alternatively, instead of dividing the data into size classes of equal range, the data may be divided in size classes of unequal range but equal number of data points (Thomson *et al.*, 1996). We have used both methodologies. After carrying out these procedures, the data were split into maximum BSI for small and large species. Thus, the splitting point between the left and the right side of the triangle was set at the body size at which the highest BSI value was observed (*c.* 10 kg, Fig. 1). This data point was included in both analyses to avoid correlation biases.

Regression statistics for all intervals used (Table 2) show a consistent pattern of negative values for the slope of the upper boundary of large species, and of positive values for small species. In the case of larger species, however, the relationships are often not significant unless the outlying data point for the elephant (*Loxodonta africana*) is deleted. Justification for deleting this data point may come from varied evidence. First, recent morphological (Grubb *et al.*, 2000) and molecular studies (Barriel *et al.*, 1999; Roca *et al.*, 2001; Debruyne *et al.*, 2003) have shown that this species includes two distantly related taxa with differentiated distribution. The forest elephant (*L. a. cyclotis*) inhabits the rain forest biome, whereas the savanna elephant (*L. a. africana*) inhabits the rest of the species range. This finding supports proposals that both forms may be actually different species. If this is the case, our data on BSI of the elephant should be modified (the savanna elephant has a BSI value of 5, instead of 6; and the value for the forest elephant is 1), which would affect our results. Secondly, the behaviour of elephants has important consequences for their ability to exploit the resources of biomes that otherwise would be out of their reach. This becomes clear in the arid regions of their distribution range, where elephants can track the presence of seasonal and permanent water sources over large areas and long periods of time (Rodgers & Elder, 1977; Blake *et al.*, 2003). Finally, this is the only species that modifies, at a large scale, the conditions of its environment (Laws, 1970; Croze *et al.*, 1981; Ben-Shahar, 1993; Dudley, 2000). Indeed, it has been suggested that the presence of proboscideans has influenced the evolution of tropical ecosystems (Cristoffer & Peres, 2003).

There is a significant relationship between body mass and BSI as judged by the sign tests of the phylogenetically independent contrasts (Table 3). Nevertheless, when magnitudes of the contrasts are considered, the regressions through the origin (Table 4) show different results depending on the method used (nested or non-nested contrasts). In general, the phylogenetic analyses appear to support a positive relationship between body size and biomic specialization; although this result is somewhat obscured, probably because the relationship is polygonal rather than lineal.

Table 2 Statistics for the relationship between maximum BSI (number of inhabited biomes) and body size ($\log_{10}$ body size in g) of African large mammals using the procedures of Blackburn *et al.* (1992; equal range of body size class) and Thomson *et al.* (1996; equal number of species in each size class)

	Small species					Large species					Large species (without *Loxodonta*)				
I	*n*	*a*	*b*	r^2	*P*	*n*	*a*	*b*	r^2	*P*	*n*	*a*	*b*	r^2	*P*
Equal range of body size class															
6	3	1.215	1.571	0.873	0.232	4	11.697	−0.975	0.668	0.183	4	14.122	−1.498	0.953	**0.024**
7	4	0.629	1.712	0.843	0.082	4	11.697	−0.975	0.668	0.183	4	14.122	−1.498	0.953	**0.024**
8	4	0.724	1.642	0.774	0.120	5	11.661	−0.970	0.681	0.086	5	14.142	−1.501	0.955	**0.004**
9	5	0.776	1.663	0.882	**0.018**	5	11.299	−0.959	0.475	0.198	5	13.924	−1.506	0.813	**0.036**
10	5	0.523	1.699	0.769	0.051	6	11.046	−0.916	0.509	0.111	6	13.259	−1.392	0.812	**0.014**
11	6	−0.099	1.866	0.843	**0.010**	6	12.526	−1.199	0.529	0.101	6	15.053	−1.722	0.825	**0.012**
12	6	−0.148	1.887	0.850	**0.009**	7	13.376	−1.452	0.467	0.090	7	15.583	−1.913	0.698	**0.019**
13	6	−1.635	2.322	0.825	**0.012**	8	13.680	−1.497	0.488	0.054	8	15.892	−1.959	0.709	**0.009**
14	7	−1.502	2.270	0.849	**0.003**	8	12.965	−1.418	0.403	0.091	8	15.258	−1.891	0.626	**0.019**
15	7	−1.551	2.292	0.854	**0.003**	9	10.880	−0.977	0.337	0.101	9	15.057	−1.865	0.673	**0.007**
Equal number of species															
6	4	−3.857	2.885	0.981	**0.010**	3	11.005	−0.774	0.966	0.118	3	13.618	−1.369	0.997	**0.035**
7	4	−3.760	2.870	0.992	**0.004**	4	10.208	−0.649	0.809	0.100	4	12.638	−1.208	0.916	**0.043**
8	5	−4.689	3.092	0.958	**0.004**	4	10.208	−0.649	0.809	0.100	4	12.638	−1.208	0.916	**0.043**
9	5	−4.689	3.092	0.958	**0.004**	5	10.165	−0.645	0.804	**0.039**	5	12.680	−1.212	0.915	**0.011**
10	6	−2.342	2.476	0.864	**0.007**	5	10.165	−0.645	0.804	**0.039**	5	12.680	−1.212	0.915	**0.011**
11	6	−2.250	2.429	0.863	**0.007**	6	10.213	−0.766	0.280	0.280	6	12.708	−1.329	0.563	0.086
12	7	0.327	1.589	0.422	0.115	6	9.759	−0.662	0.333	0.231	6	12.254	−1.215	0.665	**0.048**
13	7	−2.521	2.522	0.886	**0.002**	7	10.241	−0.727	0.450	0.099	7	12.556	−1.245	0.744	**0.012**
14	8	1.911	1.161	0.363	0.114	7	9.877	−0.674	0.334	0.174	7	12.402	−1.229	0.649	**0.029**
15	8	0.247	1.742	0.718	**0.008**	8	9.793	−0.660	0.351	0.122	8	12.076	−1.170	0.650	**0.016**

I, number of intervals; *a*, intercept; *b*, slope; r^2, determination coefficient; *P*, significance (significant relationships are in bold).

Table 3 Relationship between body size ($\log_{10}$ body size in g), BSI (number of inhabited biomes), and range size ($\log_{10}$ latitudinal extent in latitude degrees), assessed by sign test under nested contrasts (below the diagonal) and non-nested contrasts (above the diagonal) analyses

	Body size				BSI				Range size			
	n	n_p	n_n	P	n	n_p	n_n	P	n	n_p	n_n	P
Body size					109	54	31	0.017	109	62	44	0.098
BSI	210	107	74	0.017					96	81	15	< 0.001
Range size	210	124	84	0.007	212	166	46	< 0.001				

n, Number of contrasts analysed; n_p, number of positive contrasts; n_n, number of negative contrasts.

Table 4 Relationship between body size ($\log_{10}$ body size in g), BSI (number of inhabited biomes), and range size ($\log_{10}$ latitudinal extent in latitude degrees), assessed by least-squares regression through the origin under nested contrasts (below the diagonal) and non-nested contrasts (above the diagonal) analyses

	Body size			BSI			Range size		
	n	r^2	P	n	r^2	P	n	r^2	P
Body size				109	0.03	0.060	109	0.03	0.093
BSI	210	0.05	0.002				96	0.44	< 0.001
Range size	210	0.04	0.002	212	0.34	< 0.001			

n, Number of contrasts analysed.

Relationship between range size and body size

The relationship between latitudinal extent and body mass for all species of large mammals in Africa is shown in Fig. 2. There is a weak, albeit statistically significant, positive correlation ($r = 0.197$, $P = 0.002$, $n = 242$) but again the data are better described by a polygonal than a linear relationship. The upper boundary of this triangle is relatively well defined, but the other two boundaries are much less so. In order to test statistically the form of the lower boundaries of this polygonal relationship, we followed the procedures described above. The data in Fig. 2 are divided into size classes, selecting for use in a regression those points with the lowest values of latitudinal extent in each size class. We have again used both methodologies of point selection for regression (Blackburn *et al.*, 1992; Thomson *et al.*, 1996) and a range of interval numbers from 6 to 15. After carrying out these procedures, the data were split into minimum latitudinal extent for small and large species. The splitting point for body size was that at which the smallest latitudinal extent value was observed (*c.* 10 kg, Fig. 2), and again this data point was included in both analyses.

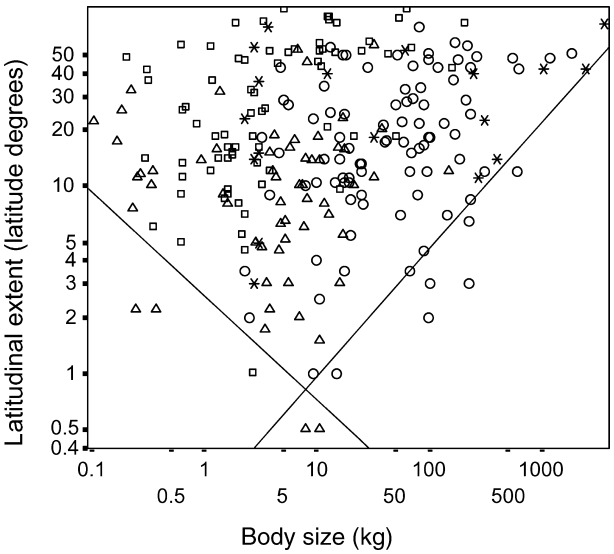

Figure 2 The relationship between latitudinal extent of geographical ranges (latitude degrees) and body mass (kg) for the African large mammals. Triangles, Primates; squares, Carnivora; circles, Artodactyla; stars, other orders. Regression lines corresponding to the analyses in Table 5 are shown (15 intervals of equal range of body size class).

Regression statistics for all intervals used (Table 5) show a consistent pattern of positive values for the slope of the lower boundary of large species, but the relationship appears to be not significant using Thomson *et al.*'s (1996) procedure. In the case of the small species, most of the relationships are not statistically significant, regardless of the method used.

According to phylogenetically independent contrasts, there is a significant relationship between body size and latitudinal extent when we analysed the nested contrasts, but this relationship is not significant in the non-nested contrasts analyses. This is so in both the sign tests (Table 3) and the regressions through origin (Table 4). Again, as the relationship between body size and latitudinal extent is basically polygonal, the analyses of phylogenetically independent contrasts appear veiled.

Relationship between range size and biomic specialization

There is a highly statistically significant positive correlation between BSI and latitudinal extent ($r = 0.625$, $P < 0.001$, $n = 244$; Fig. 3). Nevertheless, the data also show a triangular relationship. Both the upper and lower boundaries of this triangle are relatively well defined. In this case, in order to test statistically the form of these boundaries we selected respectively for use in a regression those points with the highest and lowest values of latitudinal extent in each BSI class. Both regression lines show positive values for the slope of these boundaries (slope = 0.032, $r^2 = 0.774$, $P = 0.004$, $n = 8$, for the upper boundary; slope = 0.320, $r^2 = 0.884$, $P = 0.001$, $n = 8$, for the lower boundary). Put another way, both the

Table 5 Statistics for the relationship between minimum range size ($\log_{10}$ latitudinal extent in latitude degrees) and body size ($\log_{10}$ body size in g) of African large mammals using the procedures of Blackburn *et al.* (1992; equal range of body size class) and Thomson *et al.* (1996; equal number of species in each size class)

	Small species					Large species				
I	*n*	*a*	*b*	r^2	*P*	*n*	*a*	*b*	r^2	*P*
Equal range of body size class										
6	3	1.330	−0.410	0.970	0.110	4	−3.735	0.842	0.882	0.061
7	3	1.144	−0.527	0.666	0.392	5	−3.638	0.825	0.907	**0.012**
8	4	1.397	−0.428	0.959	**0.014**	5	−3.855	0.894	0.943	**0.006**
9	4	1.397	−0.428	0.973	**0.014**	6	−3.352	0.756	0.965	< **0.001**
10	5	1.246	−0.330	0.278	0.361	6	−2.446	0.606	0.728	**0.031**
11	5	2.173	−0.628	0.770	0.051	7	−3.076	0.713	0.935	< **0.001**
12	6	2.411	−0.678	0.730	**0.030**	7	−2.774	0.685	0.755	**0.011**
13	6	2.366	−0.646	0.606	0.068	8	−3.143	0.745	0.857	**0.001**
14	6	2.443	−0.664	0.554	0.090	9	−2.958	0.711	0.808	**0.001**
15	7	2.080	−0.561	0.472	0.088	9	−2.750	0.680	0.731	**0.003**
Equal number of species in each size class										
6	3	1.330	−0.410	0.970	0.110	4	−2.682	0.631	0.834	0.087
7	4	1.216	−0.349	0.637	0.202	4	−2.475	0.575	0.934	**0.034**
8	4	1.216	−0.349	0.637	0.202	5	−1.499	0.376	0.436	0.225
9	4	1.311	−0.359	0.373	0.389	6	−2.571	0.606	0.626	0.061
10	5	1.709	−0.476	0.601	0.124	6	−1.623	0.411	0.459	0.140
11	5	1.709	−0.476	0.601	0.124	7	−2.013	0.493	0.437	0.106
12	6	1.253	−0.293	0.146	0.455	7	−1.158	0.329	0.216	0.293
13	6	1.519	−0.382	0.232	0.333	8	−2.850	0.697	0.636	**0.018**
14	7	1.404	−0.347	0.330	0.177	8	−1.911	0.512	0.425	0.080
15	7	1.388	−0.328	0.222	0.286	9	−2.133	0.541	0.442	0.051

I, number of intervals; *a*, intercept; *b*, slope; r^2, determination coefficient; *P*, significance (significant relationships are in bold).

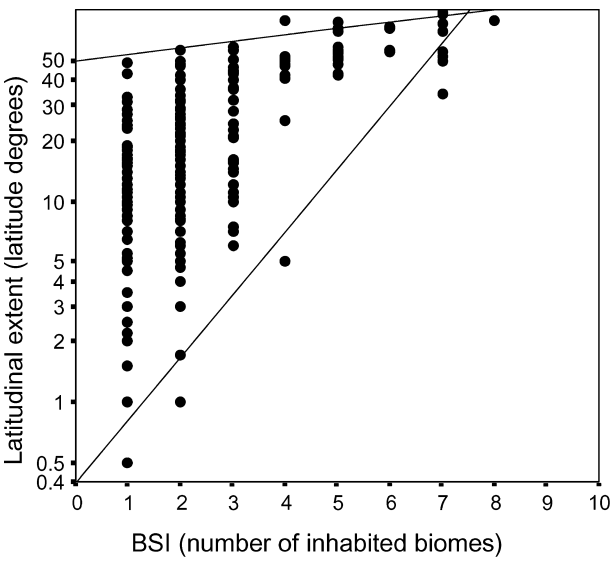

Figure 3 The relationship between biomic specialization (BSI; number of inhabited biomes) and latitudinal extent of geographical ranges (latitude degrees) for the large mammals in Africa. Regression lines define the upper and lower limits of the polygonal relationship (see text).

minimum and maximum latitudinal extent of African large mammals in a BSI class increases with the decrease of specialization.

The phylogenetically independent contrasts also indicate that the relationship between BSI and latitudinal extent is consistent and highly significant within taxa regardless of the method used (Tables 3 and 4).

DISCUSSION

Relationship between biomic specialization and body size

The polygonal relationship between biomic specialization and body size may arise from constraints that set each of the sides. Because large-bodied species disperse more rapidly and with higher rate of successful establishment in a new area (Gaston & Blackburn, 1996a), they may come to occupy a greater proportion of their potential inhabitable biomes. This could explain the trend of body mass increase with decrease in specialization that is evident in the left part of Fig. 1. But this trend is truncated and reversed in large-bodied species. In this case, the limiting factors to expansion may be the increasing need of larger species for enough food of sufficient quality (Burness *et al.*, 2002; Maurer, 2002; Midgley *et al.*, 2002; Olff *et al.*, 2002), which is unavailable in some biomes. We tested the following prediction: species that are of medium size (5–100 kg) and eurybiomic (BSI ≥ 5) should be able to inhabit biomes with lower net primary productivity (NPP, a quanti-

tative measure of food availability) than can large-bodied species (> 100 kg). Hernández Fernández & Vrba (in press) have defined eurybiomic species as those that are able to inhabit five or more different biomes because they must confront very different environmental conditions both thermally (e.g. from tropical rain forest to temperate evergreen forest) and hydrically (e.g. from rain forest to desert). We obtained mean NPP measures for biomes from Schultz (1995) and, for each one of the relevant species, recorded the minimum mean NPP among the biomes it inhabits. A *t*-test shows a statistically significant difference between the set of minimum mean NPP values of biomes inhabited by large-bodied species on the one hand, and that of biomes inhabited by medium-sized, eurybiomic species on the other hand ($t = -4.729$, $P < 0.001$, $n = 55$). Large-bodied species on average do not inhabit biomes with mean NPP as low as do eurybiomic medium-sized species (Fig. 4).

Relationship between range size and body size

Across all species, African large mammals show a roughly triangular relationship between latitudinal extent and body mass, with medium-sized species showing both small and large ranges, and large-bodied species tending to have only large ranges. Although small-bodied display an ample range of latitudinal extent, it seems that large geographical range sizes are more usual. Such a triangular relationship has been reported previously in other faunal assemblages and it is hypothesized to arise from constraints setting each of the three sides (Brown & Maurer, 1987, 1989).

The upper boundary apparently is set by the maximum latitudinal amplitude of Africa, with only a few species able to expand their ranges outside of the continent. Although the number of African species that inhabit areas outside Africa is bigger, only four of them have ranges that expand the whole continent – *Mellivora capensis*, *Panthera pardus*, *Lutra lutra*, and *Herpestes ichneumon* – all of which are carnivores. Possibly the degree of specialization required to be able to live and feed on the very different plant species inhabiting the climatic extremes of the African continent prevents the existence of herbivore species with extremely large range sizes. Meanwhile, the available food for carnivores in different biomes is still basically meat, although it belongs to different prey species. In the African continent, only the elephant (*Loxodonta africana*) has comparable latitudinal amplitude. The rock hyrax (*Procavia capensis*) has similar latitudinal amplitude but it does not inhabit the rain forest biome. Both species are characteristically generalists in their habitat and diet requirements.

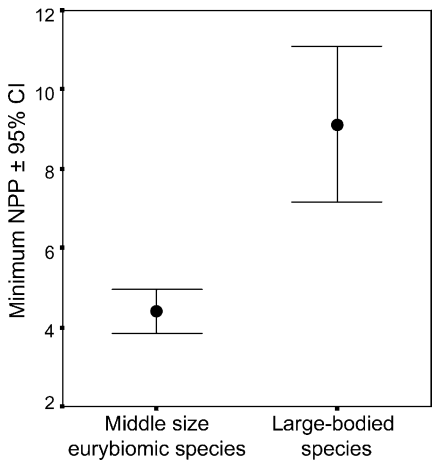

Figure 4 Minimum mean net primary production (NPP; tons per hectare and year) observed in biomes inhabited by middle-sized eurybiomic species (5–100 kg, BSI ≥ 5; $n = 19$) and large-bodied species (> 100 kg; $n = 36$). For each of the relevant species we recorded the minimum mean NPP among the biomes it inhabits. NPP measures are derived from Schultz (1995).

Several mechanisms have been proposed as determinants of the lower right boundary (Gaston & Blackburn, 1996b), but currently the most favoured one proposes that the minimum geographical range size at a given body size is fixed by the area needed to support the minimum viable global population of a species of that body size (Brown & Maurer, 1987, 1989; Taylor & Gotelly, 1994; Olifiers *et al.*, 2004). Nevertheless, the statistical significance of this boundary in the African assemblage of large mammals changes depending on the method used to test it, which suggests that other factors might be important to explain it.

In other groups of organisms, the left boundary of the range size–body size relationship is usually vertical and set by the minimum body size possible for the taxon (Brown & Maurer, 1987; Blackburn & Gaston, 1996). Nevertheless, our assemblage does not include all the groups of land mammals in Africa. The empty space in the lower left corner of Fig. 2 should be filled by species in the orders Rodentia, Insectivora, Macroscelidea and Lagomorpha. It is striking, however, that all the large mammals smaller than 2 kg belong to either Primates or Carnivora, which occupy an ecological niche different from that of most small mammals. Carnivores are predators, whereas primates are essentially arboreal omnivore species. Carnivore species have larger home ranges than omnivores of the same mass, which in turn had larger home ranges than herbivores (Mace & Harvey, 1983; Kelt & Van Vuren, 2001; Jetz *et al.*, 2004). This pattern likely reflects differing densities of food items for these groups (McNab, 1963; Harestad & Bunnell, 1979). As species with large home ranges are constrained to have low population densities, such species must have large geographical range sizes to sustain populations large enough to avoid extinction due to demographic stochasticity.

Relationship between range size and biomic specialization

Widespread mammalian species almost always occupy a large number of different biomes, but they constitute a very small fraction of the total number of mammalian species (Hernández Fernández & Vrba, 2005a, in press). The majority of African large mammals live in a narrow geographical area and

usually in only one or two biomes (Fig. 3). A similar result was found for North American mammals by Pagel *et al.* (1991), although they used habitat zones instead of biomes. James & Shine (2000) also found comparable results for the relationship between climatic specialization and range size in Australian lizards. Additionally, a negative relationship between range size and habitat specialization has been reported for the British herbaceous flora (Thompson *et al.*, 1998).

Our results are perhaps not surprising given the apparent relationship between species range size and ecological specialization; species which are able to exploit a wide variety of resources tend to be more widespread than more specialized species (Mayr, 1963; MacArthur, 1972; Jackson, 1974; Glazier, 1980; Brown, 1984, 1995). However, for a given number of inhabited biomes, the variation in latitudinal extent is often large (Fig. 3), which is related to the size of the climatic dominion the species inhabit. While specialist species that inhabit small climatic dominions (e.g. the Cape fynbos) are confined to a very small latitudinal extent, biomic specialists inhabiting large climatic dominions (e.g. the Angolo-Zambezian woodland) can occupy large range sizes.

For example, Fig. 5 shows the relationship between the latitudinal extent of stenobiomic species (BSI = 1) and the size of the climatic dominions they inhabit. A positive relationship is apparent ($r = 0.376$, $P < 0.001$). Nevertheless, it is possible to obtain additional interpretations by studying the species that are clear outliers. Several inhabitants of the riparian forests of the Lower Tana River are in this situation (*Cephalophus adersi*, *Procolobus rufomitratus* and *Cercocebus galeritus*). They are restricted to this area, which is characterized by an evergreen forest dependent on groundwater supplied by the river and surrounded by deciduous woodlands. The closest relatives of the primate species are inhabitants of the Zaire Basin rain forest. Similarly, most of the closest relatives of the Ader's duiker inhabit the rain forest biome or the most humid areas of the tropical deciduous woodland biome. This suggests a vicariant origin for these three species, associated with the Neogene-Quaternary retraction of the African rain forest biome. The rest of species in the lower part of Fig. 5 are also vicariant species whose sister clades inhabit larger areas, either within the same biome or in a different biome that resembles the ecological characteristics of their restricted range. In the first situation we find the stenobiomic species that inhabit the region between the Lower Niger and the Sanaga rivers in south-eastern Nigeria and western Cameroon (*Arctocebus calabarensis*, *Euoticus pallidus*, *Cercopithecus erythrotis*, *Cercopithecus preussi*, *Cercopithecus sclateri*, *Mandrillus leucophaeus*, and *Procolobus preussi*), and *Madoqua piacentini* in the Horn of Africa. In the second case we find *Cercopithecus solatus*, which inhabits the Ogooué River area (a very humid area of the deciduous woodland biome). One of its closest relatives, *C. lhoesti*, inhabits the Zaire Basin; the other is *C. preussi*, which inhabits south-eastern Nigeria and western Cameroon as noted above. While *Heterohyrax antineae* is restricted to the Hoggar massif (central Sahara), its sister species, *H. brucei*, inhabits a much larger range in the eastern Sahara, the deserts and savannas from the Horn of Africa and the deciduous woodlands of eastern and southern Africa. *Hippotragus leucophaeus* was an inhabitant of the Cape area, but their closest relatives, *H. equinus* and *H. niger*, inhabit the woodland biome. *Dorcatragus megalotis* and *Damaliscus hunteri* occur in relatively humid areas of the Horn of Africa whereas their closets relatives (respectively, species of *Raphicerus* and *Damaliscus*) inhabit more humid biomes.

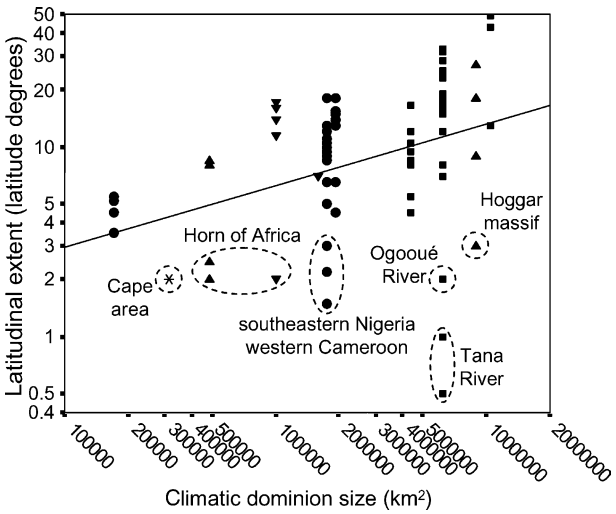

Figure 5 The relationship between latitudinal extent of geographical ranges (latitude degrees) in the stenobiomic (BSI = 1) large mammals in Africa and the size (km^2) of the climatic dominion they inhabit ($r^2 = 0.141$, $P < 0.001$). The main geographical areas clustering restricted-range species are shown. Circles, evergreen tropical rain forest; squares, tropical deciduous woodland; downward triangles, savanna; upward triangles, subtropical desert; stars, sclerophyllous woodland-shrubland.

It is striking that the geographical occurrence of all these species is limited to a few particular areas in the continent (Fig. 5), which suggest that the process of splitting of geographical ranges (vicariance) is associated with particular characteristics of some areas and their associated historical factors. Recently, Hernández Fernández & Vrba (in press) have shown that the initiating causes of the modern pattern of frequency distribution in biome specialization should be sought in those long-term historical factors that have, over the past few millions of years, influenced rates of species vicariance and of speciation. Their findings agree with the resource use hypothesis (Vrba, 1987) and related habitat theory (Vrba, 1992, 1995, 1999), which suggest that the key to present-day macroecological patterns is found in the past: in the long-term history of turnover (speciation, extinction) of clades, and in the palaeoclimatic and other geological changes of the areas in which the clades evolved. Their predictions include generally higher rates of vicariance and speciation over the past few millions of years in those biomes that have suffered major contraction and expansion associated with climatic changes (particularly, in Africa these biomes are the rain forest and desert biomes, and secondarily the tropical deciduous woodland). It also predicts that biome specialists

are much more frequent than biome generalists, because they had higher rates of vicariance and speciation (Vrba, 1987). Our results for Africa appear to be consistent with each of these predictions. In agreement with previous studies (Pagel *et al.*, 1991; Ricklefs & Schluter, 1993; Blackburn & Gaston, 1996; Ruggiero *et al.*, 1998; Hernández Fernández & Vrba, 2005a, in press), our results indicate that the biogeographical structure and history of the continent have a major influence in the macroecological patterns reported because they generate major constraints on evolutionary and ecological processes.

CONCLUSIONS

Although it seems that body mass is correlated with both biomic specialization and range size, the associations are weak and inconsistent across different methodological approaches. Our results indicate a polygonal rather than lineal relationship. They suggest that although body size is of central importance in life history and ecology for mammals and other organisms (Peters, 1983), its role in establishment of degree of specialization and geographical range size appears modulated by other factors, such as environmental productivity, diet, population genetics, dispersal capabilities, biogeographical structure, history of the continent, etc. Nevertheless, many of the factors that may play a role in causing differences in specialization and range size (e.g. environmental tolerance, dietary niche breadth and dispersal abilities) are also somehow related to body size (Jarman, 1974; Rapoport, 1975; Lindstedt & Boyce, 1985; Cristoffer, 1987; Marquet *et al.*, 1995; Gordon & Illius, 1996; Kelt & Van Vuren, 1999; Brashares *et al.*, 2000; Gagnon & Chew, 2000; Harcourt, 2000). This will complicate the recognition of general causal relationships between the factors studied here.

Although the numbers of published studies reporting macroecological patterns are constantly increasing, there are still major patterns structuring the ecological assemblages that have not been documented (Gaston & Blackburn, 1999). Our results show that, although biomic specialization and range size may be closely related, their independent study highlights how different factors influence their relationship with body size. It is obvious that the study of general patterns in ecological attributes other than those classically studied (e.g. body size, range size, abundance) will draw attention to new paths in the research for causality in ecological processes. In order to study and compare these new macroecological patterns between different geographical regions and groups, ecologists need measures of ecological attributes, such as the BSI, that can be applied worldwide and to very dissimilar taxa.

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SUPPLEMENTARY MATERIAL

The following material is available from: http://www.blackwellpublishing.com/products/journals/suppmat/JBI/JBI1270/JBI1270sm.htm

Appendix S1 Phylogeny of the African large mammals.

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BIOSKETCHES

Manuel Hernández Fernández has a broad interest in the area of evolutionary ecology, encompassing a wide variety of problems related to the biological and climatic evolution of the Neogene-Quaternary Earth. He is particularly interested in the interface between macroecology and palaeoclimatology. Further information is available at http://www.ucm.es/info/paleo/personal/hdezfdez.htm.

Elisabeth S. Vrba has research interests in the field of palaeontology and macroevolution, with particular emphasis on the development of the African mammal faunas during the Neogene. One of her major goals is to discover new patterns in the palaeontological record, and to use them to make original contributions to evolutionary theory.

Editor: Robert Whittaker

Figure A1 (General)

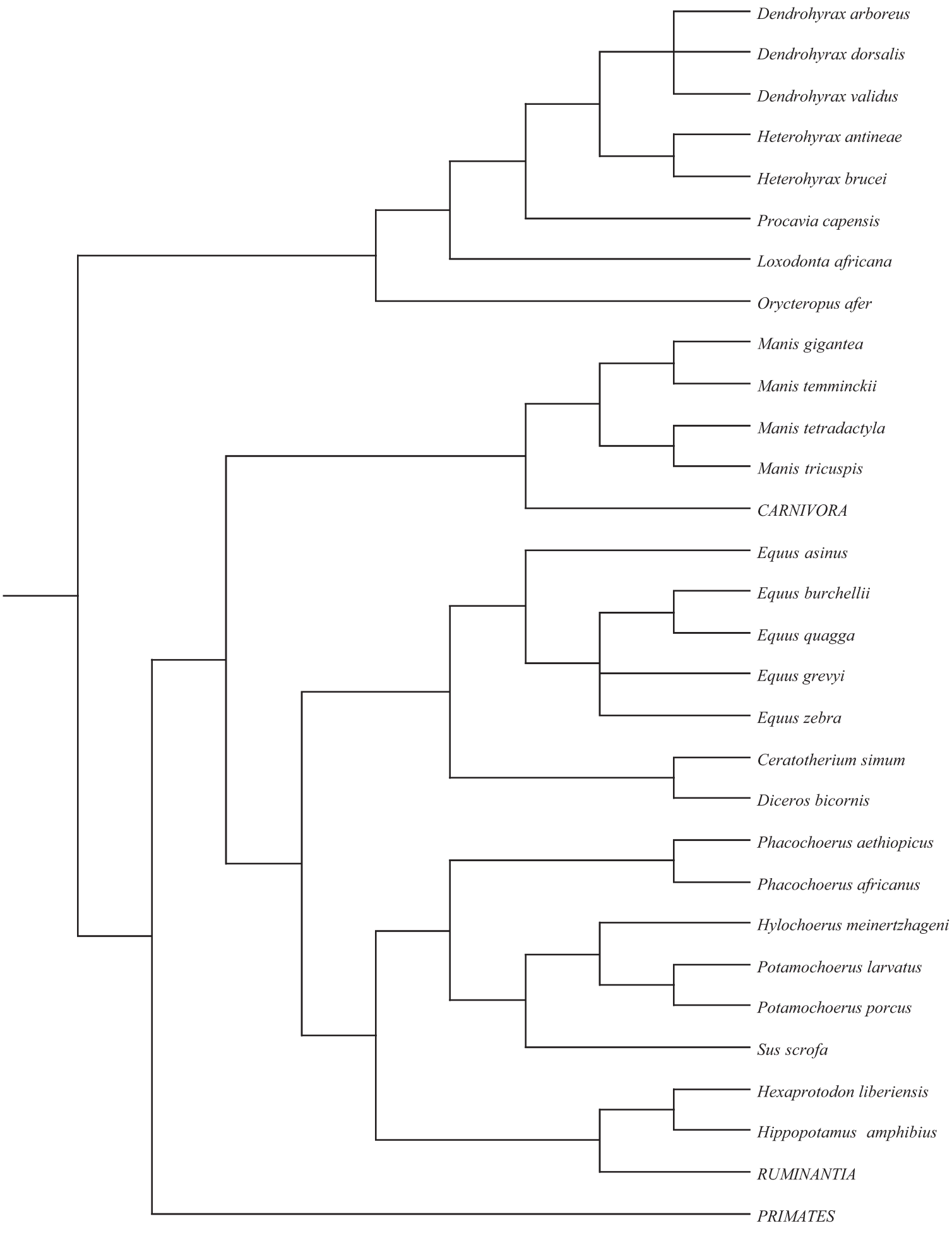

Figure A2 (Carnivora)

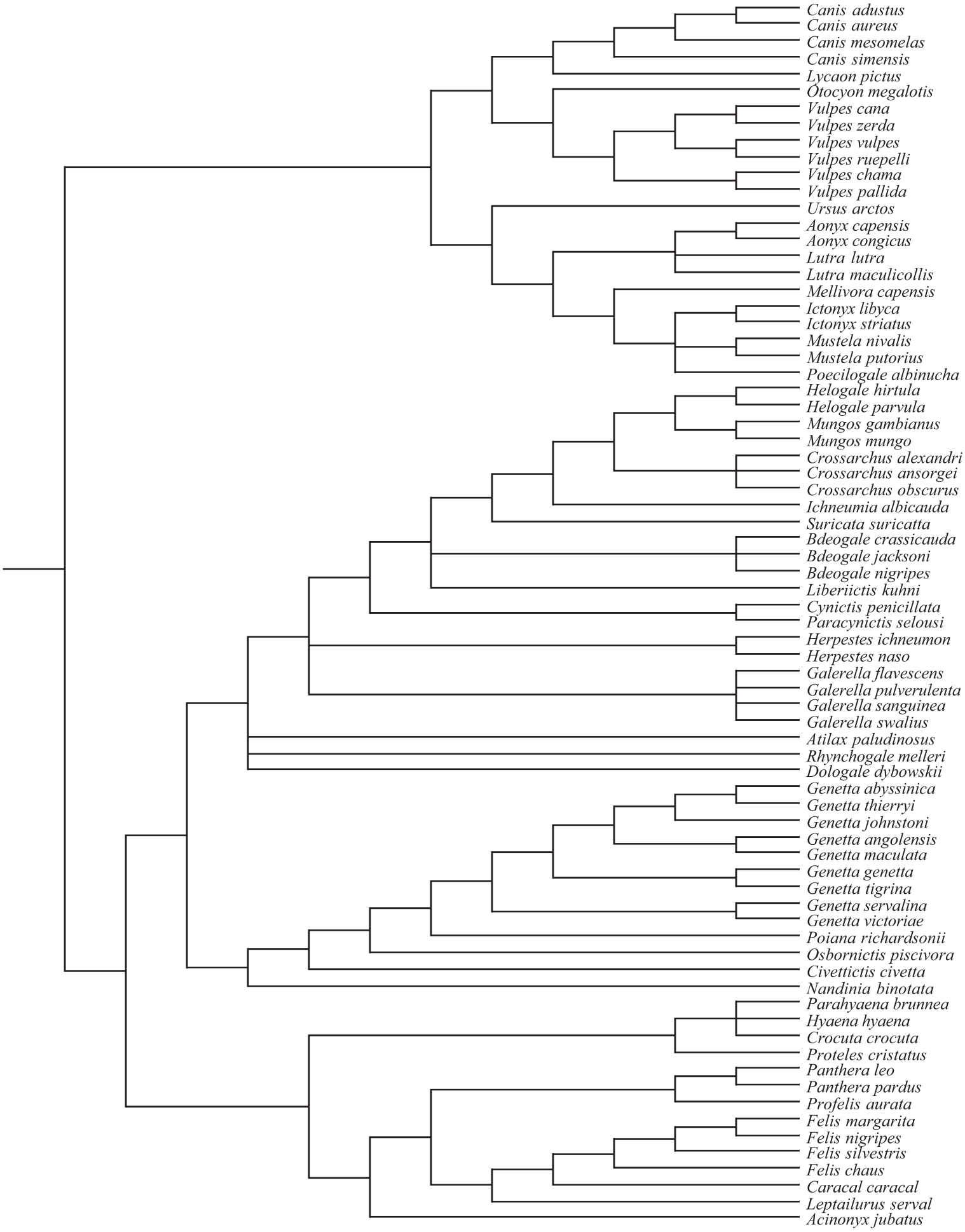

Figure A3 (Ruminantia)

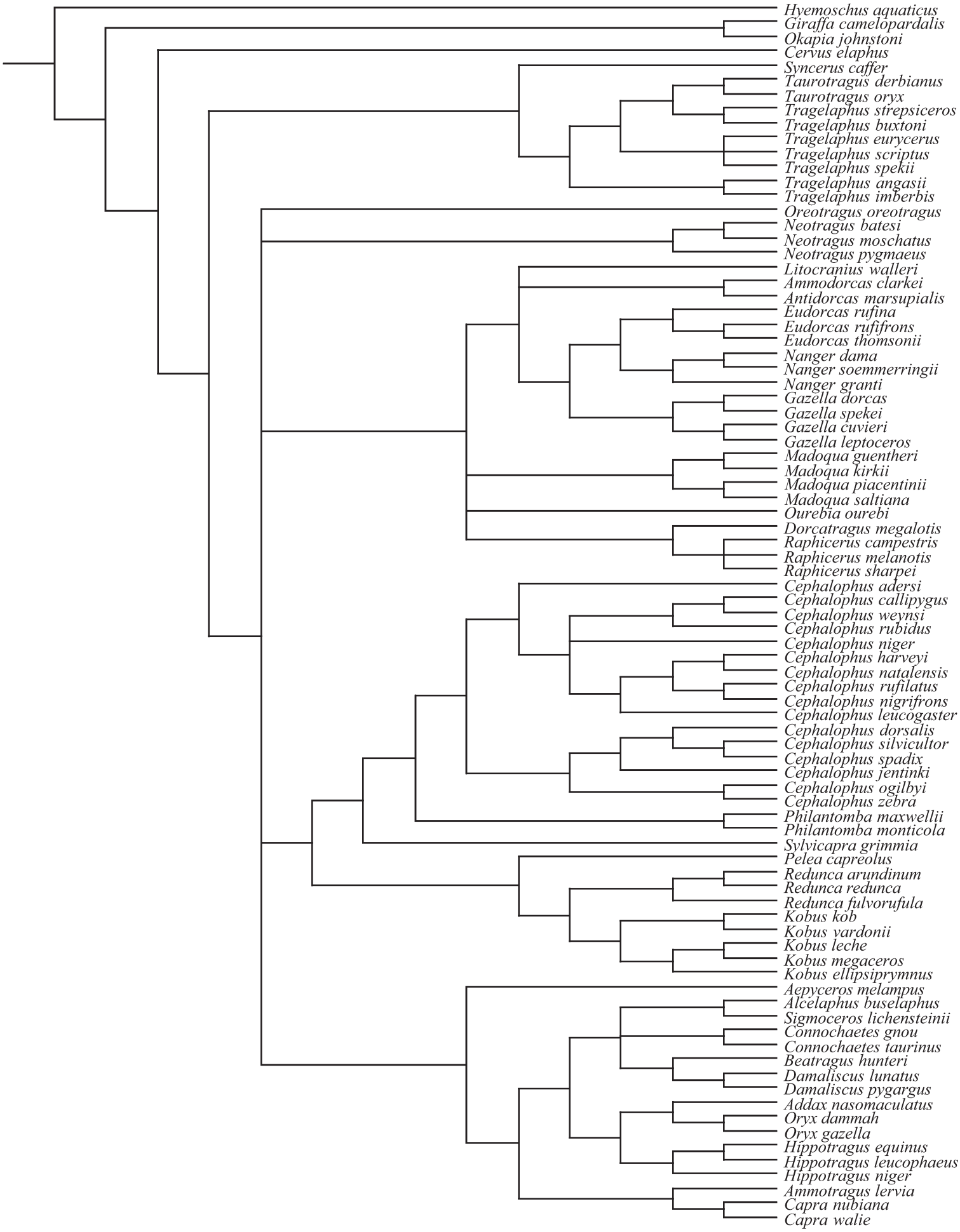
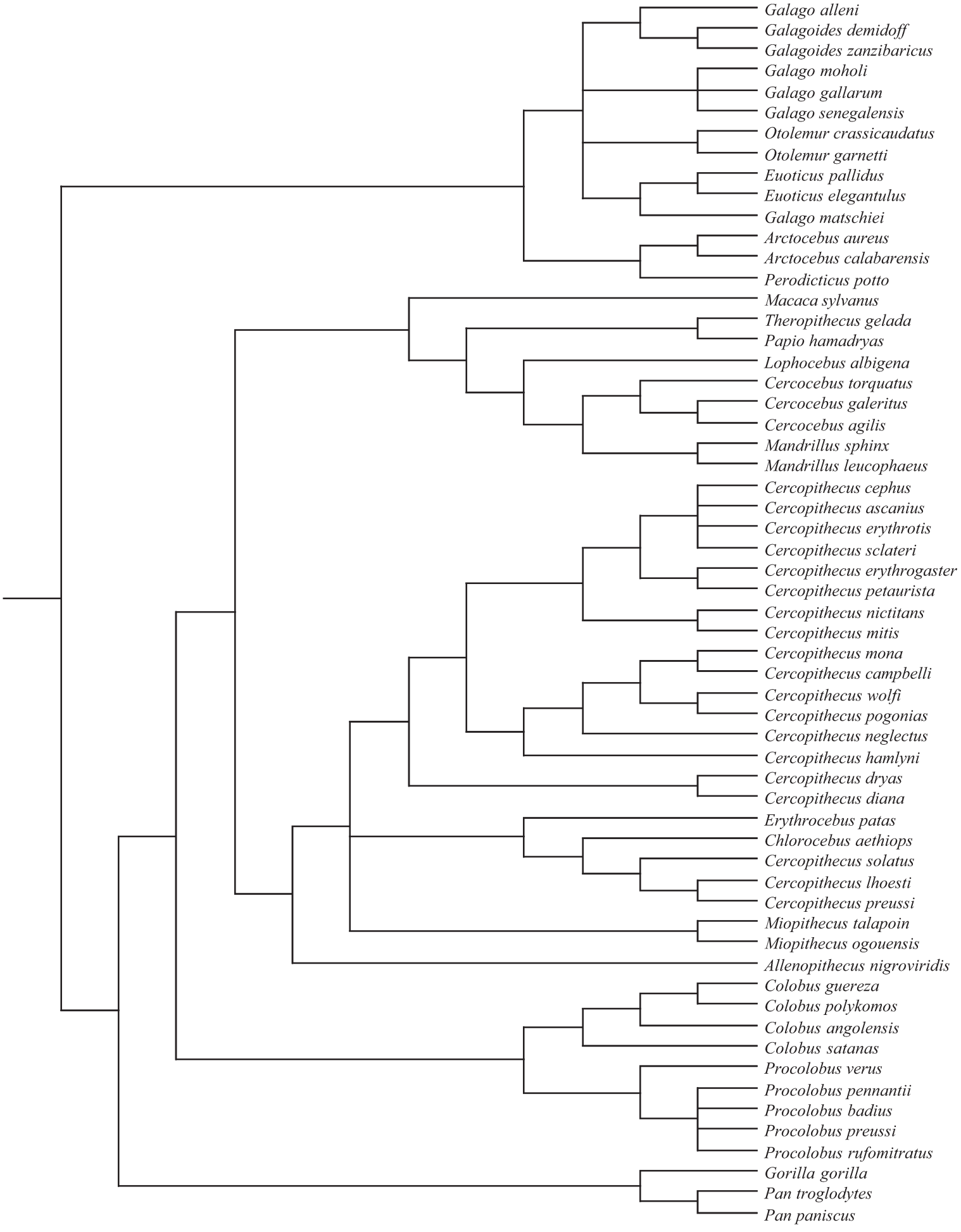
Figure A4 (Primates)