

Ecological correlates of ghost lineages in ruminants

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Abstract.—Integration between phylogenetic systematics and paleontological data has proved to be an effective method for identifying periods that lack fossil evidence in the evolutionary history of clades. In this study we aim to analyze whether there is any correlation between various ecomorphological variables and the duration of these underrepresented portions of lineages, which we call ghost lineages for simplicity, in ruminants. Analyses within phylogenetic (Generalized Estimating Equations) and non-phylogenetic (ANOVAs and Pearson correlations) frameworks were performed on the whole phylogeny of this suborder of Cetartiodactyla (Mammalia). This is the first time ghost lineages are focused in this way. To test the robustness of our data, we compared the magnitude of ghost lineages among different continents and among phylogenies pruned at different ages (4, 8, 12, 16, and 20 Ma). Differences in mean ghost lineage were not significantly related to either geographic or temporal factors. Our results indicate that the proportion of the known fossil record in ruminants appears to be influenced by the preservation potential of the bone remains in different environments. Furthermore, large geographical ranges of species increase the likelihood of preservation.

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Accepted: 3 March 2011

Supplementary materials deposited at Dryad: doi: 10.5061/dryad.80n50

Introduction

An important part of our knowledge about evolution is based on information from fossils. Patterns of preservation in the fossil record have provided a key tool for estimating dates of appearance of new living forms on Earth and understanding events of diversification and extinction (Norell 1993). Nevertheless, our comprehension of the many factors that may influence the preservation of species in the fossil record is still incomplete. For example, although stratigraphic sampling appears to be relevant (Alroy et al. 2001; Crampton et al. 2003), we do not know whether ecological characteristics of species are also important in this context. The use of ecological data on modern species along with phylogenetic systematics synthesizing information from both extant and extinct species may provide a novel approach to this issue.

Traditionally, cladistic hypotheses have been adjusted to stratigraphic ranges of species

by adding inferred lineages for which no fossil has been recovered. Following this view, ghost lineages were defined as complete branches in an evolutionary tree that lacks a known fossil record, but whose presence is inferred from the tree topology obtained by phylogenetic analysis (Norell 1992; Smith 1994). These ghost lineages can be recovered only by a phylogenetic approach calibrated with paleontological data (Norell 1996). Moreover, Smith (1994) also identified range extensions, which are temporal gaps that must be added to the stratigraphic ranges of taxa in order to build an evolutionary tree that fits temporal relationships with a phylogenetic analysis. In this context some authors have surveyed the extent to which assumptions of different cladistic hypotheses may influence the estimations of our paleontological knowledge (Norell and Novacek 1992a,b; Weishampel 1996; O'Keefe and Sander 1999; Benton et al. 2000; Wagner 2000a,b; Wills 2002; Pol and Norell 2006;

Worthy et al. 2006). For example, given two fossil taxa with different first appearances and known fossil ranges that do not overlap, different lengths of inferred range must be added depending on different cladistic assumptions. If we assume that as organisms evolve they give rise to new taxa in dichotomous splits, the evolutionary histories of two sister groups sharing a common ancestor should have equal duration (Paul 1982). Thus, a range from the first appearance of the younger taxon to the date of first appearance of the older taxon must be added (Norell 1996). Conversely, an ancestor-descendant relationship could be assumed and we would only have to infer a range between the last appearance of the older taxon (inferred ancestor) and the first appearance of the younger taxon (Wagner 1995; 2000a,b). In phylogenies containing fossil taxa, cladistic hypotheses and temporal calibration come from the same source: fossils. In such cases sampling bias directly affects phylogenetic accuracy, which in turn may bias the assessment of the fossil record. Only well-resolved topologies yield a correct interpretation of gaps in the fossil record (Wagner 2000a).

Molecular phylogenies provide a new tool in this scenario. Molecular-based phylogenetic analyses usually generate origin dates earlier than the first appearance of known fossil taxa (Hartenberger 1998; Adkins et al. 2001; Huchon et al. 2002; Teeling et al. 2005). Comparing both fossil and molecular estimates of lineages origin may shed some light on the accuracy with which the fossil record represents the evolutionary history of lineages leading to living species (Teeling et al. 2005; Johnson et al. 2006). This approach, according to the criteria of Teeling et al. (2005), places the oldest known fossil for each branch of the molecular tree and calculates the percentage of unrepresented basal branch length. Nevertheless, although taxonomic sampling bias in molecular trees of extant species is theoretically smaller than in phylogenies of extinct taxa, assessing the accuracy of the fossil record in this manner is applicable only to lineages leading to extant species and it is not exempt from limitations (see further discussion in "Limitations of the Methods," below).

For the sake of simplicity, hereafter we use the term "ghost lineages" to refer to ghost lineages, range extensions, and unrepresented basal branch lengths. All of these have been included in studies assessing the congruence among divergence dates from molecular phylogenies and fossil ranges (Teeling et al. 2005; Johnson et al. 2006), paleodiversity estimates (Lane et al. 2005), inferences about patterns of character acquisition (Sidor and Hopson 1998), and the magnitude of critical events (Cavin and Forey 2007; Ruta and Benton 2008). In this work, we tested whether several ecomorphological attributes of the species (body mass, presence in biomes, range size, diet, and locomotor modes) may influence the duration of ghost lineages and, therefore, the likelihood of generating a complete fossil record. Our test focused on the suborder Ruminantia, which is the most speciose extant clade of large land herbivores and presents a fossil record that covers a time span of 50 Myr. Ruminants have developed a spectacular diversity of ecomorphological specializations, with wide geographical and ecotypic ranges and existing species inhabiting every terrestrial biome (Walter 1970). Such ecological diversity and taxonomic richness, with 197 extant species in 79 genera and about 300 extinct genera (Grubb 1993; McKenna and Bell 1997; Hernández Fernández and Vrba 2005a), prove ruminants to be a valuable target for evolutionary research (Vrba and Schaller 2000).

Materials and Methods

Data.—The phylogeny of suborder Ruminantia was taken from the supertree published by Hernández Fernández and Vrba (2005a), which includes all the 197 extant and recently extinct ruminant species. This supertree is a consensus tree combining morphological, ethological and molecular information from every phylogeny published up to date, and includes a time calibration using paleontological data (Fig. 1).

To identify the correlations among ghost lineages' durations and the different ecomorphological characters, we compiled data for 19 binary variables and two continuous variables (Table 1). Following Teeling et al.

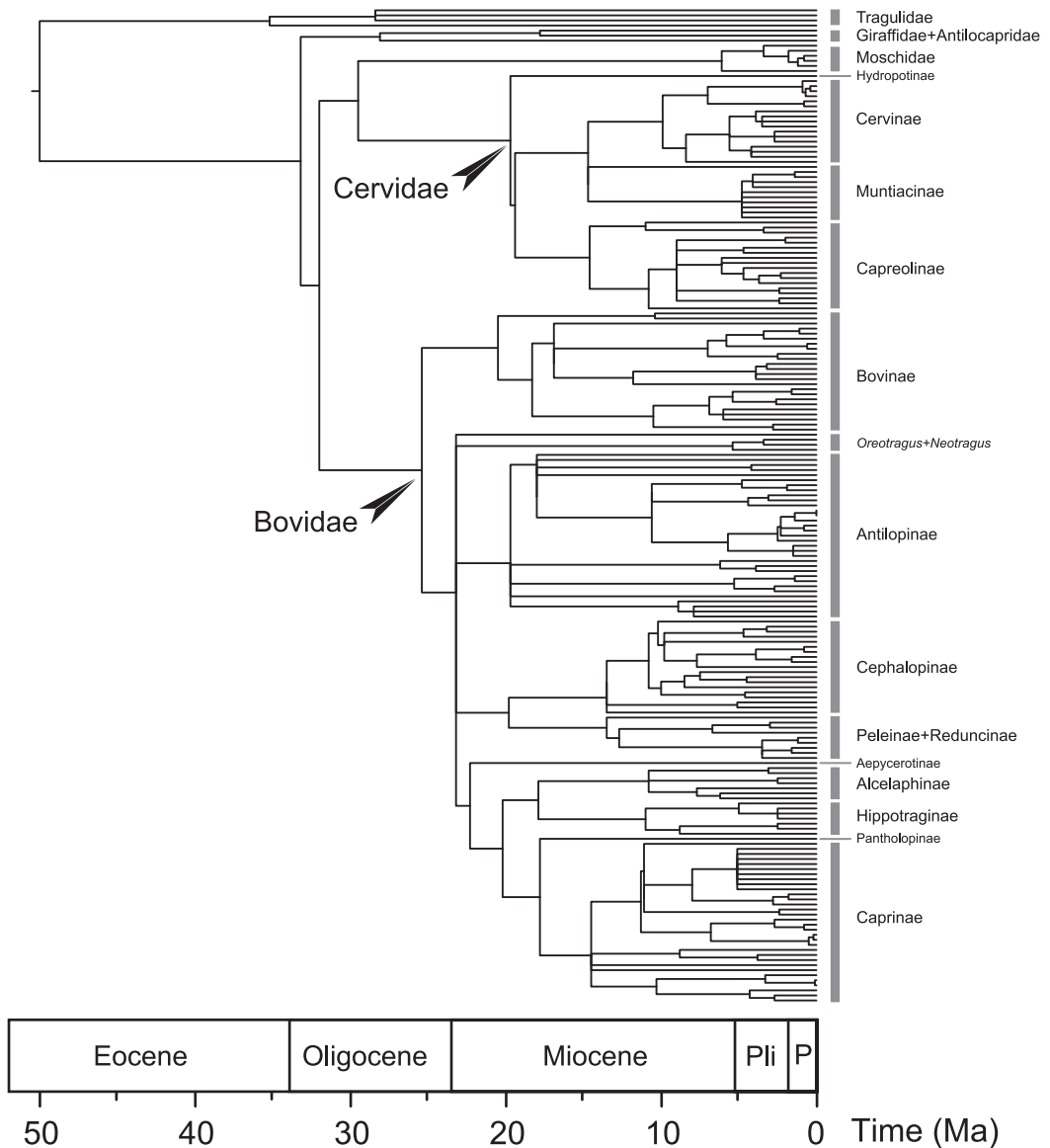


FIGURE 1. Supertree of all 197 extant and recently extinct species of ruminants (Hernández Fernández and Vrba 2005a) showing the names of families and subfamilies.

(2005) we collated the oldest known fossil for each branch of the supertree and compared its age with the ages representing the beginning and end of that branch (see table in Appendix 1 and figures in Appendix 2, in the online supplemental material). We calculated ghost lineage durations as the percentage of the total branch length that contains no fossil record. Unlike Johnson et al.'s (2006) study, in which, for example, "an old *Lynx* species fossil was interpreted as representing the

entire fossil history of this group (i.e., 0% missing)," we used each fossil for calculating the underrepresented length of only one branch.

Information on body mass was compiled for the 197 extant species of the group. We also differentiated five locomotor modes (Alcalde et al. 2006) and three diets (DeMiguel et al. 2008). Biogeographic data for the 197 species were taken from distribution information obtained from several sources (Ansell 1971;

TABLE 1. Variables used in the non-phylogenetic and the phylogenetic analyses of ghost lineage percentages.

		Variable			
Continuous		Binary			
Body mass (Kg)	Range extension (latitude extent)	Locomotor mode	Diet	Biomes	Stenobiomy
		Gallop	Browser	Evergreen tropical rain forest (I)	Species inhabiting only one biome
		Zigzag	Mixed	Deciduous tropical forest (II)	
		Bounding	Grazer	Savanna (II/III)	
		gallop		Subtropical desert (III)	
		Stotting		Mediterranean forest (IV)	
		Climbing		Temperate evergreen forest (V)	
				Temperate broad-leaf deciduous forest (VI)	
				Steppe and cold desert (VII)	
				Boreal coniferous forest (Taiga) (VIII)	
				Tundra (IX)	

Corbet 1978; Hall 1981; Eisenberg 1989; Corbet and Hill 1992; Redford and Eisenberg 1992; Grubb 1993; Kingdon 1997; Mitchell-Jones et al. 1999; Eisenberg and Redford 2000). We used the method described by Hernández Fernández (2001) to estimate the presence/absence in the terrestrial biomes described by Walter (1970), who defined them as particular combinations of climate and vegetation. Because altitudinal gradients represent a habitat series analogous to that of biomes, vegetation belts in mountains were also borne in mind when estimating the occurrence of species in a given biome (Hernández Fernández and Vrba 2005c). Furthermore, following Hernández Fernández and Vrba (2005b) we considered as stenobiomic species those occupying only one biome.

To test the correlation between ghost lineage durations and the different ecomorphological variables, we performed both non-phylogenetic and phylogenetic tests.

Non-Phylogenetic Test.—We conducted conventional analyses treating all branches in the supertree as cases (356 in total). Ghost lineage percentages for each branch were assessed as explained above, and values of the independent variables were reconstructed by using parsimony reconstruction methods as implemented in Mesquite (Maddison and Maddison 2007). When character reconstruction was ambiguous for binary variables (both “0” and “1” values were equally parsimonious in some branch of the tree) we used the “most parsimonious reconstruction mode” and chose

those reconstructions with the most gains (changes from “0” to “1”) and the fewest losses (changes from “1” to “0”), and those with the fewest gains and the most losses. We carried out our analyses for both of them (Ortolani and Caro 1996; Ortolani 1999). To gauge relationships between ghost lineage percentage and the continuous and binary ecomorphological variables, we used Pearson correlations and one-factor ANOVAs, respectively.

Phylogenetic Test.—Closely related species are more likely to share similar ecological features because of common ancestry, so data for different species cannot be considered as independent points in comparative studies (Felsenstein, 1985; Harvey & Pagel, 1991). Therefore, by using the comparative method in a phylogenetic framework, we avoid phylogenetic biases that might be present in our ecological variables. Phylogenetic analyses were performed using Generalized Estimating Equations (GEE) (Paradis and Claude 2002; Paradis 2006), which incorporates species relatedness as a correlation matrix and uses a generalized linear model approach. Because data for these analyses must be introduced for the tips of the tree, we calculated for each tip of the tree the average of the values of ghost lineage percentage of every branch leading to that tip from the root of the tree.

Tests for Data Robustness.—It may be argued that some clades exhibit a great deal of ghost range because they are all located in one part of the world or are all of a particular age,

which could be related to differential paleontological sampling. In order to address this issue we conducted two different ANOVA tests. The first one compared the ghost lineage percentages of the branches implied in the evolution of ruminant species from different continents (North America, South America, Eurasia, and Africa). The second analysis compared ghost lineage percentages among the branches of the ruminant phylogeny when pruned at different ages (4, 8, 12, 16 and 20 Ma) to establish whether ghost lineages were more important in some geologic ages than others. We did not use phylogenies pruned at ages older than 20 Ma because the number of branches implied in the analyses would be too low to develop statistically powerful analyses.

Furthermore, as an additional test for the robustness of the data on ghost lineage length, we performed linear regression analyses between the ghost lineage percentages of the branches and the age of their previous node. A statistically strong relationship would indicate that the age of the branch may influence the importance of the ghost range in it. We analyzed the four continental data sets as well as the complete data set.

Limitations of the Methods.—Because the phylogeny used for the analyses is a supertree, it could change as new phylogenetic studies are published (see, for example, the case of the supertree for mammalian families [Liu et al. 2001; Bininda-Emonds et al. 2007]). Our results are therefore contingent on the degree to which future studies affect the interpretation of phylogenetic relationships within Ruminantia. Nevertheless, future variations in the topology or higher resolution of the tree will have little influence on our conclusions as long as such changes do not affect many branches. Taking into account the high number of studies Hernández Fernández and Vrba (2005a) used to develop the ruminant supertree, as well as the supertree's high consistency and retention indices, profound changes in the topology of the tree are unlikely in the near future.

Another possible drawback is related to the selection of fossils for the definition of ghost lineages in every branch. Some uncertainty in the phylogenetic relationships of extinct taxa is warranted and the position of single taxa along

the ruminant phylogeny may affect the inference of ghost lineage durations. This issue, however, is also dependent on the development of new studies on phylogenetic relationships of extinct ruminants, including the occurrence of new discoveries. Such uncertainty cannot be accounted for in this work, but future reviews of our conclusions may be needed in order to confirm their robustness.

Finally, our estimate of the duration of ghost lineages for ruminants might differ substantially from one that considers the entire fossil record of the clade, because including more taxa and branches could lead to differences in the calculation of ghost lineages. Such a problem could be solved by using a complete supertree, one that also includes all the extinct taxa of Ruminantia. Although the development of such a new supertree is in progress, however, it is beyond the scope of the current study.

Results

Data Robustness.—The results of the post hoc ANOVAs for different ages point to a slight difference between the current percentages of ghost lineage in extant lineages and those at 4 Ma. Nevertheless, the results from 0 and 4 Ma didn't differ significantly from any of the other time periods (Fig. 2).

The relationship between ghost lineage percentage in each branch and the age of the prior node does not fit a linear model, neither for the whole tree, or when the lineages are examined separately on each continent (Figs. 3, 4), with the exception of Eurasia. Nevertheless, in the latter case this relationship is very weak, explaining less than 4% of the variability in the data set.

Finally, the post hoc ANOVAs did not show any significant differences when ghost lineage percentages of each continent were compared ($p = 0.593$) (Fig. 5).

All these results indicate that our data on ghost lineage percentage are not influenced by either geographical or temporal factors.

Ghost Lineages and their Ecological Correlates.—The total percentage of ghost lineage in Ruminantia, measured as the proportion of ghost lineage durations and total range, is 80% (Table 2). Average durations of ghost lineages

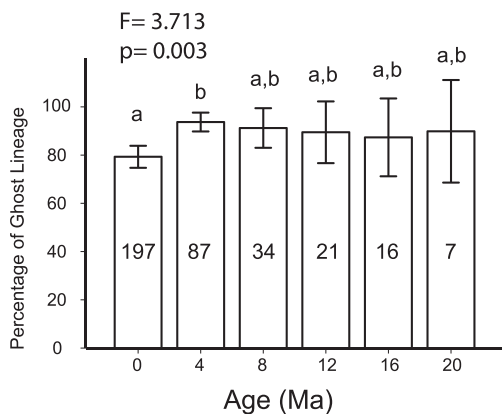


FIGURE 2. Variation of the average ghost lineage percentages at different ages. Number of tips for each age is shown within the bars. Error bars: 95% confidence interval.

for each family and subfamily range from 11%, in the lineage that gave rise to the only species included in the modern Antilocapridae (*Antilocapra americana*), to 97.5% in Hydropotinae (Table 2).

Pearson correlations and one-factor ANOVAs showed significant relationships between ghost lineage percentage and ten ecomorphological variables. Negative correlations were found between ghost lineages percentages and body mass, geographic range, gallop, stotting, grazer diet, and presence in savannahs. Therefore, it seems that all these variables are associated with a better representation in the known fossil record. On the other hand, positive correlations were found for zigzag, bounding gallop, browser diet, and presence in tropical rain forest (biome I) (Table 3).

The phylogenetic analyses confirm several of these trends (Table 3). They corroborate negative correlations between ghost lineage presence and both geographic range extension and presence in savannahs. Moreover, they also verify positive correlations with zigzag locomotor mode and presence in evergreen tropical rain forests.

To confine our conclusions to the most consistent results, below we discuss only the correlations showing significance in both the non-phylogenetic and the phylogenetic tests.

Discussion

Total Ghost Lineage Percentage for Ruminantia.—Our calculations yielded 80% of ghost lineage

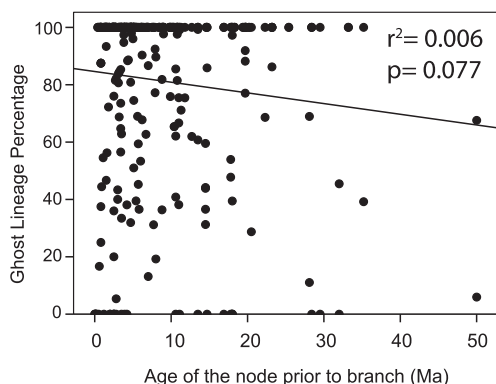


FIGURE 3. Relationship between the age of each branch of the supertree of ruminants and the associated ghost lineage percentage. The determination coefficient and significance of the linear regression are shown.

for the supertree of the 197 extant and recently extinct species of ruminants. This does not necessarily imply a poor fossil record. In fact, Ruminantia have one of the most abundant fossil records associated with any mammalian group. Therefore, our results suggest that the known fossil record of ruminants is not intimately related to the evolution of extant species. That is, many extinct lineages of ruminants are not closely related to extant species and, consequently, were not included in the calculations of ghost lineage percentages.

In any case, this value is similar to those estimated by Teeling et al. (2005) for 30 genera inside Chiroptera (73%) and by Johnson et al. (2006) for the 37 living species of Felidae (76%). The slightly higher value of ghost lineage percentage for Ruminantia may be related to two different issues. First, it follows the positive correlation between the number of tips in a tree and the global percentage of ghost lineage ($r = 0.198$, $p < 0.001$, according to the analyses of 1000 trees included in the supplementary data of Benton et al. 2000). In fact, if we downsample our data to the genus level (79 tips), the mean percentage of ghost lineage in ruminants decreases to 70.7%, which seems to indicate a substantially better fossil record than the ones for Chiroptera and Felidae. Second, it also might be caused by the exclusion from the calculations of fossil taxa that pre-dated the molecular age of the associated branch and whose relatedness to the earlier lineage was unclear, unlike in the

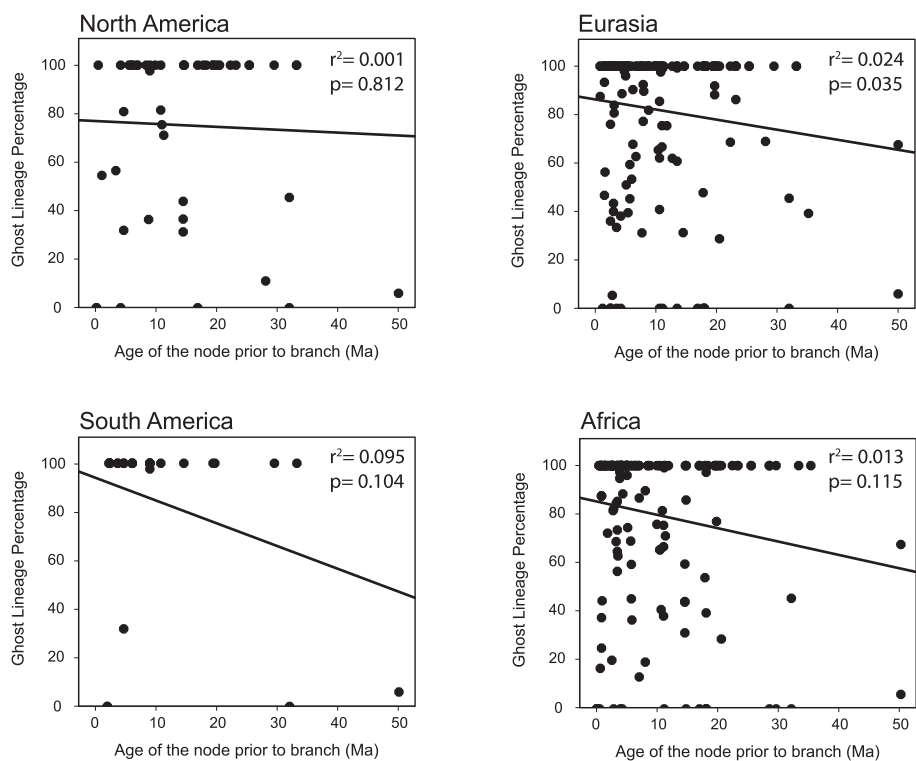


FIGURE 4. Relationship between the age of each branch and the associated ghost lineage percentage analyzed separately for the extant species from each continent. For each linear regression, the determination coefficient and the significance of the relationship are shown.

analyses of Teeling et al. (2005) and Johnson et al. (2006). As described in our methods, we used each fossil for the calculations of the unrepresented proportion of a single branch, whereas in some cases Johnson et al. (2006) based an assessment of 0% unrepresented

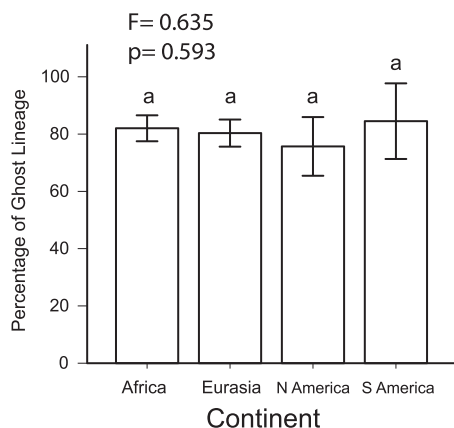


FIGURE 5. Ghost lineage percentages inferred in the evolution of ruminant species from different continents. Error bars: 95% confidence interval.

lineage length in several adjacent branches on a single fossil.

Ecological Variables Enhancing the Probability of Preservation in the Fossil Record (Negative Correlations).—The study showed a significant relationship between gallop locomotor mode and low percentages of ghost lineage. Gallop is associated with open substrates with scant or grassy vegetation. In these types of substrates, edaphic activity and acidity from dead leaves are usually absent, and thus conditions are more favorable for preservation of fossil bones (Table 3).

In the same way, those species exhibiting wide latitudinal ranges are understood to be widespread; thus, because they are more likely to appear in fossils sites, we might have a more complete knowledge of their evolutionary history. It has been argued that widespread species are usually larger and more generalist than species with restricted ranges (Mayr 1963; MacArthur 1972; Jackson 1974; Glazier 1980; Brown 1984, 1995; Brown

TABLE 2. Total percentage and mean percentage of ghost lineage (%GL) for different taxonomic groups in Ruminantia. Sp, number of extant species; B, number of branches.

Family	Sp	B	Total GL%	Mean GL%	Subfamily	Sp	B	Total GL%	Mean GL%
Tragulidae	4	6	81.55	72.40					
Antilocapridae	1	1	11.03	11.03					
Giraffidae	2	3	33.99	38.89					
Moschidae	6	11	46.77	90.90					
Cervidae	47	80	90.18	82.44	Hydropotinae	1	1	97.5	97.5
					Cervinae	18	33	90.01	76.85
					Muntiacinae	10	13	97.36	93.39
					Capreolinae	18	31	85.11	82.18
Bovidae	137	249	83.57	80.74	Bovinae	24	46	82.32	78.92
					Antilopinae	33	58	84.99	81.18
					Cephalophinae	19	36	98.26	95.83
					Peleinae	1	1	60.74	60.74
					Reduncinae	8	15	70.00	66.50
					Aepycerotinae	1	1	68.61	68.61
					Alcelaphinae	7	12	73.94	73.94
					Hippotraginae	7	12	81.47	76.70
					Pantholopinae	1	1	53.93	53.93
					Caprinae	32	53	80.04	75.40
					<i>incertae sedis</i>	4	6	94.20	97.70
TOTAL	197	356	80.30	81.50					

and Maurer 1987, 1989; Gaston and Blackburn 1996a,b; Thompson et al. 1998). Nevertheless, the relationships among these ecomorphological factors are highly variable (Hernández Fernández and Vrba 2005b), which could explain why our results indicate consistent statistical significance between ghost lineage percentage and range extent, but not with other apparently related variables.

According to our results, the presence in the biome savannah seems to underlie the congruence between stratigraphic and phylogenetic information. Savannahs are generally located in sedimentary basins where rainfall is highly seasonal and thus wildlife is attracted to marginal lacustrine environments. Although savannahs are typically associated with the formation of fossils sites (Behrensmeyer 1976; Lyman 1994; Polonio and López Martínez 2000; Alberdi et al. 2001), this biome has developed substantially during the late Neogene (Potts and Behrensmeyer 1992; Hernández Fernández and Vrba 2006). The origin of savannah environments like those found today has been associated with the spread of C_4 grasses in the late Miocene (Cerling et al. 1993). We must clarify that in this work we do not refer to biomes as geographical areas but as ecosystems, which are prone to latitudinal shift due to global climatic changes. In this sense herbivore

species are not constrained to particular geographic areas but rather are adapted to vegetation types; ruminants especially are usually assumed to have occurred in the same habitats across climatic changes, although they were forced to shift their geographic ranges pursuing the shifts of biomes (Vrba 1987; Hernández Fernández and Vrba 2005b; Moreno-Bofarull et al. 2008).

Ecological Variables Decreasing the Probability of Preservation in the Fossil Record (Positive Correlations).—Only one of all the ecomorphological variables studied in this work is consistently identified by both phylogenetic and non-phylogenetic analyses as having a significant influence on the decrease of preservation probability within the fossil record of ruminants. There is a significant correlation (marginally significant in the phylogenetic analysis) between high percentages of ghost lineages and the presence in the evergreen tropical rain forest (biome I). This biome type is usually found in locations with dense forest canopy, which hinders finding fossil sites. Finally, these locations are in areas not much studied from a paleontological point of view (Kerbis et al. 1993).

Zigzag locomotion mode showed a significant or marginally significant positive correlation with ghost lineage percentage. Adaptations

TABLE 3. Significance level (p) of the relationships between ghost lineage percentage and the ecomorphological variables under study (Table 1) yielded from both the conventional and the phylogenetic tests. Some variables are duplicated (denoted by ".2"), representing the most-parsimonious reconstructions for the inner branches of the tree with more losses and more gains, respectively (see methods). Bold-italic, significant correlation ($p < 0.05$); italic, marginal significance ($p < 0.1$); +, positive relationship; -, negative relationship; NA, not available.

	Non-phylogenetic		Phylogenetic	
	356 branches		197 species	
Body mass	0.014	-	0.106	+
Log (body mass)	0.000	-	0.924	+
Range extension	0.000	-	0.002	-
Log (range)	0.001	-	0.004	-
Gallop	0.000	-	0.074	-
Gallop.2	0.001	-	(NA)	
Zigzag	0.005	+	0.019	+
Zigzag.2	0.007	+	(NA)	
Bounding gallop	0.018	+	0.476	+
Bounding gallop.2	0.004	+	(NA)	
Stotting	0.022	-	0.608	-
Stotting.2	0.027	-	(NA)	
Climbing	0.619	-	0.156	+
Browser	0.008	+	0.810	-
Browser.2	0.005	+	(NA)	
Mixed diet	0.878	-	0.580	-
Mixed diet.2	0.414	-	(NA)	
Grazer	0.002	-	0.403	+
Grazer.2	0.010	-	(NA)	
I	0.139	+	0.061	+
I.2	0.043	+	(NA)	
II	0.692	-	0.786	+
II.2	0.673	+	(NA)	
II/III	0.037	-	0.013	-
II/III.2	0.008	-	(NA)	
III	0.801	-	0.960	-
III.2	0.092	-	(NA)	
IV	0.561	-	0.738	+
IV.2	0.665	-	(NA)	
V	0.350	+	0.313	+
V.2	0.202	+	(NA)	
VI	0.696	-	0.288	+
VII	0.380	+	0.111	+
VII.2	0.698	+	(NA)	
VIII	0.631	+	0.740	-
VIII.2	0.977	+	(NA)	
IX	0.286	-	0.689	-
IX.2	0.510	-	(NA)	
Stenobiomic	0.159	+	0.403	+
Stenobiomic.2	0.232	+	(NA)	

to different locomotor modes reflect the type of environment inhabited by each species (Smith and Savage 1956; Köhler 1993; DeGusta and Vrba 2003). In this way, zigzagging is related to forests characterized by developed undergrowth and intense soil activity due to the presence of roots, fungi, microorganisms, and soil fauna (Walter 1970). All these factors make preservation of organic remains difficult.

Conclusions

The study of ghost lineages and the causes of their existence and duration are still barely explored. To tackle this issue we applied the Generalized Estimating Equations, ANOVAs and Pearson correlations to phylogenetic data on ruminants. Our intent was to clarify whether biometric, biogeographic, or ecological variables our knowledge of ruminant paleontology and phylogeny, as well as how these factors influence the fit between paleontological and phylogenetic data within this suborder.

The results indicate that the proportion of the known fossil record of ruminants is determined largely by the potential for bone preservation in each environment. The likelihood of such preservation is also correlated with geographical distribution.

Additional analyses studying ghost lineages and their duration patterns along phylogenies of different groups could shed light on the biases that affect our knowledge of the fossil record. Finally, comprehensive studies of the species' ecomorphological characteristics (Hernández Fernández et al. 2009) in the global fossil record of those groups could help us to test hypotheses generated by studies of modern ruminant species.

Acknowledgments

We thank B. Luna (Universidad de Castilla-La Mancha), A. Arias Royo (Museo Nacional de Ciencias Naturales, CSIC), and A. Moreno Bofarull (Universidad Complutense de Madrid) for providing us with distribution data for European and South American ruminants. M. S. Domingo (Museo Nacional de Ciencias Naturales, CSIC) and L. Domingo (Universidad Complutense de Madrid) made interesting comments and offered valuable feedback on taphonomy and isotopic studies. Comments by D. L. Fox (University of Minnesota), M. Benton (University of Bristol), and J. Marcot (University of Illinois) were very helpful and improved the final version of the manuscript. We are also thankful to M. T. Lavandeira for her assistance with the English of the original manuscript.

This research was made possible by grants from the Spanish Ministry of Science and

Innovation (CGL2006-01773/BTE, CGL2008-05813-C02-01/BTE and CGL2010-19116/BOS) and from the Complutensian University of Madrid (PR1/06-14470-B). We acknowledge additional financial support from the UCM through a grant to the Research Group UCM 910607 on Evolution of Cenozoic Mammals and Continental Palaeoenvironments. During the development of this research M.H.F. had a UCM contract from the Program "Ramón y Cajal" of the Ministerio de Educación y Ciencia of Spain.

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Appendix 1. Calculations of the Ghost Lineages Percentages for every branch of the supertree of Ruminantia. Age of Nodes and their numeration were taken from Hernández Fernández & Vrba (2005a). Number of branches according to Appendix 2.

Branch #	Node Prior to Branch	Age of Previous Node	Node After Branch	Age of Node After Branch	Oldest Fossil	Age of Oldest Fossil	Time Interval Branch	Age of Lineage	Ghost Lineage Duration	Ghost Lineage %
1	4	28.4					28.4 - 0.0	28.4	28.4	100.0
2	4	28.4					28.4 - 0.0	28.4	28.4	100.0
3	3	28.4	4	28.4			28.4 - 28.4	0	28.4	0.0
4	3	28.4					28.4 - 0.0	28.4	28.4	100.0
5	2	35.2	3	28.4			35.2 - 28.4	6.8	35.2	100.0
6	2	35.2			<i>Dorcatherium</i>	21.4	35.2 - 0.0	35.2	13.8	39.2
7	1	50	2	35.2	<i>Archaeotragulus</i>	40	50.0 - 35.2	14.8	10.0	67.6
8	7	17.8			<i>Praepalaeotragus</i>	17.8	17.8 - 0.0	17.8	0.0	0.0
9	7	17.8			<i>Bohlinia</i>	9.3	17.8 - 0.0	17.8	8.5	47.8
10	6	28.1	7	17.8	<i>Propalaeoryx/Sperrgebiotomeryx</i>	21	28.1 - 17.8	10.3	7.1	68.9
11	6	28.1			<i>Bedenomeryx milaloquensis</i>	25	28.1 - 0.0	28.1	3.1	11.0
12	5	33.2	6	28.1			33.2 - 28.1	5.1	33.2	100.0
13	14	0.8					0.8 - 0.0	0.8	0.8	100.0
14	14	0.8					0.8 - 0.0	0.8	0.8	100.0
15	13	1.3	14	0.8			1.3 - 0.8	0.5	1.3	100.0
16	13	1.3					1.3 - 0.0	1.3	1.3	100.0
17	12	1.9	13	1.3			1.9 - 1.3	0.6	1.9	100.0
18	12	1.9					1.9 - 0.0	1.9	1.9	100.0
19	11	3.5	12	1.9			3.5 - 1.9	1.6	3.5	100.0
20	11	3.5					3.5 - 0.0	3.5	3.5	100.0
21	10	6.4	11	3.5			6.4 - 3.5	2.9	6.4	100.0
22	10	6.4					6.4 - 0.0	6.4	6.4	100.0
23	9	29.5	10	6.4	<i>Dremotherium</i>	29.5	29.5 - 6.4	23.1	0.0	0.0
24	57	2.4					2.4 - 0.0	2.4	2.4	100.0
25	57	2.4					2.4 - 0.0	2.4	2.4	100.0
26	49	9	57	2.4			9.0 - 2.4	6.6	9.0	100.0
27	56	2.4					2.4 - 0.0	2.4	2.4	100.0
28	56	2.4					2.4 - 0.0	2.4	2.4	100.0
29	49	9	56	2.4			9.0 - 2.4	6.6	9.0	100.0
30	55	2.3					2.3 - 0.0	2.3	2.3	100.0
31	55	2.3					2.3 - 0.0	2.3	2.3	100.0
32	54	3.7	55	2.3			3.7 - 2.3	1.4	3.7	100.0
33	54	3.7					3.7 - 0.0	3.7	3.7	100.0
34	53	4.7	54	3.7			4.7 - 3.7	1	4.7	100.0
35	53	4.7					4.7 - 0.0	4.7	4.7	100.0

Branch #	Node Prior to Branch	Age of Previous Node	Node After Branch	Age of Node After Branch	Oldest Fossil	Age of Oldest Fossil	Time Interval Branch	Age of Lineage	Ghost Lineage Duration	Ghost Lineage %
36	52	6.1	53	4.7			6.1 - 4.7	1.4	6.1	100.0
37	52	6.1					6.1 - 0.0	6.1	6.1	100.0
38	52	6.1					6.1 - 0.0	6.1	6.1	100.0
39	49	9	52	6.1			9.0 - 6.1	2.9	8.9	100.0
40	51	4.7			<i>Odocoileus virginianus</i>	3.2	4.7 - 0.0	4.7	1.5	31.9
41	51	4.7			<i>Odocoileus hemionus</i>	0.9	4.7 - 0.0	4.7	3.8	80.9
42	49	9	51	4.7	<i>Odocoileus sp.</i>	4.8	9.0 - 4.7	4.3	4.2	97.7
43	50	2			<i>Ozotoceros</i>	2	2.0 - 0.0	2	0.0	0.0
44	50	2			<i>Antifer ensenadense</i>	2	2.0 - 0.0	2	0.0	0.0
45	49	9	50	2	<i>Eocoileus gentryorum y Bretzia pseudalces</i>	5	9.0 - 2.0	7	4.0	57.1
46	48	10.8	49	9			10.8 - 9.0	1.8	10.8	100.0
47	48	10.8			<i>Rangifer sp</i>	3	10.8 - 0.0	10.8	7.8	72.2
48	45	14.6	48	10.8			14.6 - 10.8	3.8	14.6	100.0
49	47	3.4			<i>Capreolus sussenbornensis</i>	3	3.4 - 0.0	3.4	0.4	11.8
50	47	3.4			<i>Caproelus caproelus</i>	0.5	3.4 - 0.0	3.4	2.9	85.3
51	46	11	47	3.4	<i>Procaproelus loczyi</i>	8.1	11.0 - 3.4	7.6	2.9	38.2
52	46	11			<i>Cervalces (Libralces) gallicus / Alcinae indet</i>	3	11.0 - 0.0	11	8.0	72.7
53	45	14.6	46	11			14.6 - 11.0	3.6	14.6	100.0
54	26	19.4	45	14.6			19.4 - 14.6	4.8	19.4	100.0
55	44	1.4					1.4 - 0.0	1.4	1.4	100.0
56	44	1.4					1.4 - 0.0	1.4	1.4	100.0
57	43	4.1	44	1.4			4.1 - 1.4	2.7	4.1	100.0
58	43	4.1			<i>M. muntjak</i>	0.5	4.1 - 0.0	4.1	3.6	87.8
59	43	4.1			<i>M. feae</i>	0.5	4.1 - 0.0	4.1	3.6	87.8
60	42	4.8	43	4.1			4.8 - 4.1	0.7	4.8	100.0
61	42	4.8					4.8 - 0.0	4.8	4.8	100.0
62	42	4.8					4.8 - 0.0	4.8	4.8	100.0
63	42	4.8					4.8 - 0.0	4.8	4.8	100.0
64	42	4.8			<i>M. rooselvorum</i>	0.1	4.8 - 0.0	4.8	4.7	97.9
65	42	4.8			<i>M. reevesi</i>	1.3	4.8 - 0.0	4.8	3.5	72.9
66	42	4.8					4.8 - 0.0	4.8	4.8	100.0
67	41	14.7	42	4.8	<i>Muntiacus leilaoensis</i>	8	14.7 - 4.8	9.9	6.7	67.7
68	41	14.7			<i>Elaphodus cephalophus</i>	0.5	14.7 - 0.0	14.7	14.2	96.6
69	27	14.7	41	14.7			14.7 - 14.7	0	14.7	0.0
70	40	4.2					4.2 - 0.0	4.2	4.2	100.0

Branch #	Node Prior to Branch	Age of Previous Node	Node After Branch	Age of Node After Branch	Oldest Fossil	Age of Oldest Fossil	Time Interval Branch	Age of Lineage	Ghost Lineage Duration	Ghost Lineage %
71	40	4.2			<i>C. elaphus acoronatus</i>	0.8	4.2 - 0.0	4.2	3.4	81.0
72	39	4.2	40	4.2			4.2 - 4.2	0	0.8	0.0
73	39	4.2					4.2 - 0.0	4.2	4.2	100.0
74	35	5.6	39	4.2			5.6 - 4.2	1.4	5.6	100.0
75	38	2.7					2.7 - 0.0	2.7	2.7	100.0
76	38	2.7					2.7 - 0.0	2.7	2.7	100.0
77	38	2.7					2.7 - 0.0	2.7	2.7	100.0
78	35	5.6	38	2.7	<i>Rucervus sivalensis</i>	3.6	5.6 - 2.7	2.9	2.0	69.0
79	37	3.5			<i>Rusa unicolor</i>	1.3	3.5 - 0.0	3.5	2.2	62.9
80	37	3.5			<i>R. timorensis</i>	0.1	3.5 - 0.0	3.5	3.4	97.1
81	37	3.5					3.5 - 0.0	3.5	3.5	100.0
82	36	3.9	37	3.5			3.9 - 3.5	0.4	3.9	100.0
83	36	3.9					3.9 - 0.0	3.9	3.9	100.0
84	35	5.6	36	3.9			5.6 - 3.9	1.7	5.6	100.0
85	34	8.4	35	5.6			8.4 - 5.6	2.8	8.4	100.0
86	34	8.4			<i>Elaphurus bifurcatus / Arvernoceros ardei</i>	3	8.4 - 0.0	8.4	5.4	64.3
87	28	9.9	34	8.4			9.9 - 8.4	1.5	9.9	100.0
88	33	0.8			<i>D.c. mugharensis / Dama clactoniana</i>	0.78	0.8 - 0.0	0.8	0.0	2.5
89	33	0.8			<i>Dama dama tiberina</i>	0.78	0.8 - 0.0	0.8	0.0	2.5
90	29	7	33	0.8	<i>Megacerini-Eucladoceros o Pseudodama</i>	3	7.0 - 0.8	6.2	4.0	64.5
91	32	0.4					0.4 - 0.0	0.4	0.4	100.0
92	32	0.4					0.4 - 0.0	0.4	0.4	100.0
93	31	0.7	32	0.4			0.7 - 0.4	0.3	0.7	100.0
94	31	0.7					0.7 - 0.0	0.7	0.7	100.0
95	30	3	31	0.7			3.0 - 0.7	2.3	3.0	100.0
96	30	3			<i>Axis axis fossilis / Axis shansius</i>	3	3.0 - 0.0	3	0.0	0.0
97	29	7	30	3	<i>Axis sp./ Axis speciosus</i>	6.2	7.0 - 3.0	4	0.8	20.0
98	28	9.9	29	7	<i>Cervocerus</i>	7.7	9.9 - 7.0	2.9	2.2	75.9
99	27	14.7	28	9.9			14.7 - 9.9	4.8	14.7	100.0
100	26	19.4	27	14.7			19.4 - 14.7	4.7	19.4	100.0
101	25	19.7	26	19.4			19.7 - 19.4	0.3	19.7	100.0
102	25	19.7			<i>Hydropotes inermis / Hydropotes sp</i>	0.5	19.7 - 0.0	19.7	19.2	97.5
103	9	29.5	25	19.7			29.5 - 19.7	9.8	29.5	100.0
104	8	32	9	29.5	<i>Eumeryx</i>	32	32.0 - 29.5	2.5	0.0	0.0
105	79	2.8			<i>Tragelaphus gaudryi</i>	2.65	2.8 - 0.0	2.8	0.2	5.4

Branch #	Node Prior to Branch	Age of Previous Node	Node After Branch	Age of Node After Branch	Oldest Fossil	Age of Oldest Fossil	Time Interval Branch	Age of Lineage	Ghost Lineage Duration	Ghost Lineage %
106	79	2.8					2.8 - 0.0	2.8	2.8	100.0
107	73	10.5	79	2.8			10.5 - 2.8	7.7	10.5	100.0
108	78	6					6.0 - 0.0	6	6.0	100.0
109	78	6			<i>Tragelaphus gridei</i>	2.8	6.0 - 0.0	6	3.2	53.3
110	110	4.7					4.7 - 0.0	4.7	4.7	100.0
111	74	6.9	78	6			6.9 - 6.0	0.9	6.9	100.0
112	77	2.6					2.6 - 0.0	2.6	2.6	100.0
113	77	2.6					2.6 - 0.0	2.6	2.6	100.0
114	75	5.4	77	2.6			5.4 - 2.6	2.8	5.4	100.0
115	76	1.6					1.6 - 0.0	1.6	1.6	100.0
116	76	1.6					1.6 - 0.0	1.6	1.6	100.0
117	75	5.4	76	1.6	<i>Taurotragus nakuse</i>	3.9	5.4 - 1.6	3.8	1.5	39.5
118	74	6.9	75	5.4			6.9 - 5.4	1.5	6.9	100.0
119	73	10.5	74	6.9			10.5 - 6.9	3.6	10.5	100.0
120	73	18.3	73	10.5			18.3 - 10.5	7.8	18.3	100.0
121	72	3.9					3.9 - 0.0	3.9	3.9	100.0
122	72	3.9					3.9 - 0.0	3.9	3.9	100.0
123	70	3.9	72	3.9			3.9 - 3.9	0	3.9	0.0
124	71	3.2			<i>Bubalus teilandi</i>	0.5	3.2 - 0.0	3.2	2.7	84.4
125	71	3.2			<i>Bubalus palaeokerabau</i>	1	3.2 - 0.0	3.2	2.2	68.8
126	70	3.9	71	3.2			3.9 - 3.2	0.7	3.9	100.0
127	69	11.8	70	3.9			11.8 - 3.9	7.9	11.8	100.0
128	69	11.8			<i>Syncerus sp</i>	2.9	11.8 - 0.0	11.8	8.9	75.4
129	62	16.9	69	11.8			16.9 - 11.8	5.1	16.9	100.0
130	68	2.5			<i>Bos javanicus</i>	2	2.5 - 0.0	2.5	0.5	20.0
131	68	2.5					2.5 - 0.0	2.5	2.5	100.0
132	63	7	68	2.5	<i>Leptobos falconeri</i>	3.1	7.0 - 2.5	4.5	3.9	86.7
133	67	0.6			<i>Bos primigenius</i>	0.5	0.6 - 0.0	0.6	0.1	16.7
134	67	0.6					0.6 - 0.0	0.6	0.6	100.0
135	64	5.8	67	0.6	<i>Bos acutifrons</i>	3.9	5.8 - 0.6	5.2	1.9	36.5
136	66	1.1					1.1 - 0.0	1.1	1.1	100.0
137	66	1.1			<i>Bison latifrons</i>	0.5	1.1 - 0.0	1.1	0.6	54.5
138	65	3.4	66	1.1	<i>Bison tamanensis</i>	2.1	3.4 - 1.1	2.3	1.3	56.5
139	65	3.4			<i>Bos grunniens</i>	0.9	3.4 - 0.0	3.4	2.5	73.5
140	64	5.8	65	3.4			5.8 - 3.4	2.4	5.8	100.0

Branch #	Node Prior to Branch	Age of Previous Node	Node After Branch	Age of Node After Branch	Oldest Fossil	Age of Oldest Fossil	Time Interval Branch	Age of Lineage	Ghost Lineage Duration	Ghost Lineage %
141	63	7	64	5.8			7.0 - 5.8	1.2	7.0	100.0
142	62	16.9	63	7			16.9 - 7.0	9.9	16.9	100.0
143	61	16.9	62	16.9			16.9 - 16.9	0	16.9	0.0
144	61	16.9					16.9 - 0.0	16.9	16.9	100.0
145	60	18.3	61	16.9			18.3 - 16.9	1.4	18.3	100.0
146	58	20.5	60	18.3			20.5 - 18.3	2.2	20.5	100.0
147	59	10.4			<i>Tetracerus daviesi</i>	3.6	10.4 - 0.0	10.4	6.8	65.4
148	59	10.4			<i>Boselaphus sp</i>	3.6	10.4 - 0.0	10.4	6.8	65.4
149	58	20.5	59	10.4	<i>Boselaphini indet</i>	17.6	20.5 - 10.4	10.1	2.9	28.7
150	15	25.4	58	20.5	<i>Eotragus sansanensis</i>		25.4 - 20.5	4.9	25.4	100.0
151	159	2.7					2.7 - 0.0	2.7	2.7	100.0
152	159	2.7					2.7 - 0.0	2.7	2.7	100.0
153	158	4.3	159	2.7			4.3 - 2.7	1.6	4.3	100.0
154	158	4.3			<i>Capricornis sumatrensis</i>	0.5	4.3 - 0.0	4.3	3.8	88.4
155	155	10.3	158	4.3			10.3 - 4.3	6	10.3	100.0
156	157	0.1			<i>Naemorhedus goral</i>	0.1	0.1 - 0.0	0.1	0.0	0.0
157	157	0.1			<i>Naemorhedus caudatus</i>	0.1	0.1 - 0.0	0.1	0.0	0.0
158	156	3.3	157	0.1			3.3 - 0.1	3.2	3.3	100.0
159	156	3.3					3.3 - 0.0	3.3	3.3	100.0
160	155	10.3	156	3.3			10.3 - 3.3	7	10.3	100.0
161	139	14.5	155	10.3	<i>Rupicaprini indet</i>	12	14.5 - 10.3	4.2	2.5	59.5
162	154	3.8			<i>Rupicapra rupicapra</i>	0.1	3.8 - 0.0	3.8	3.7	97.4
163	154	3.8			<i>Rupicapra pyrenaica</i>	0.2	3.8 - 0.0	3.8	3.6	94.7
164	153	8.8	154	3.8			8.8 - 3.8	5	8.8	100.0
165	153	8.8			<i>Neotragoceros</i>	5.6	8.8 - 0.0	8.8	3.2	36.4
166	139	14.5	153	8.8	<i>Rupicaprini indet</i>	12	14.5 - 8.8	5.7	2.5	43.9
167	152	0.2			<i>Ovis dalli</i>	0.2	0.2 - 0.0	0.2	0.0	0.0
168	152	0.2			<i>Ovis canadiensis</i>	0.2	0.2 - 0.0	0.2	0.0	0.0
169	151	0.5	152	0.2			0.5 - 0.2	0.3	0.5	100.0
170	151	0.5			<i>Ovis nivicola</i>	0.5	0.5 - 0.0	0.5	0.0	0.0
171	148	6.8	151	0.5			6.8 - 0.5	6.3	6.8	100.0
172	150	0.8			<i>Ovis vignei</i>	0.1	0.8 - 0.0	0.8	0.7	87.5
173	150	0.8			<i>Ovis aries</i>	0.1	0.8 - 0.0	0.8	0.7	87.5
174	149	2.7	150	0.8			2.7 - 0.8	1.9	2.7	100.0
175	149	2.7			<i>Ovis amon</i>	0.5	2.7 - 0.0	2.7	2.2	81.5

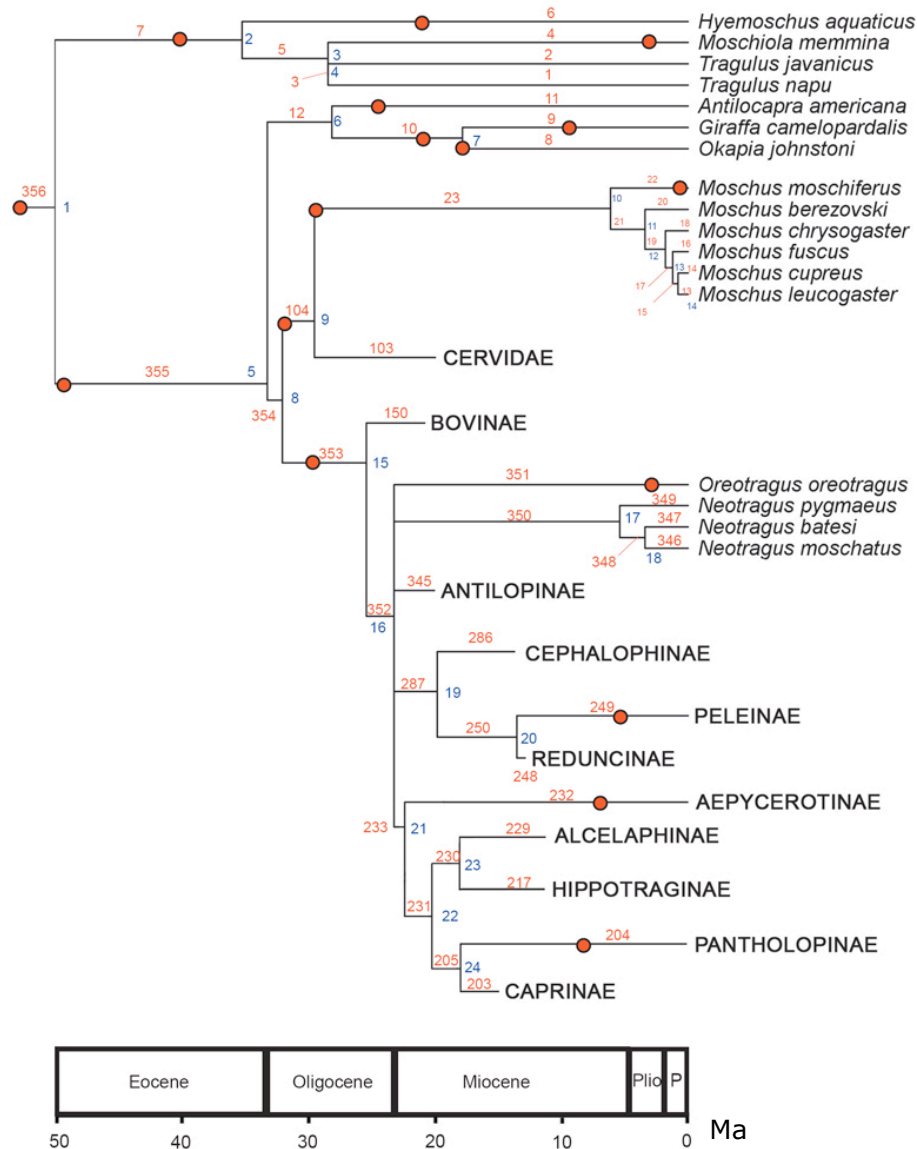
Branch #	Node Prior to Branch	Age of Previous Node	Node After Branch	Age of Node After Branch	Oldest Fossil	Age of Oldest Fossil	Time Interval Branch	Age of Lineage	Ghost Lineage Duration	Ghost Lineage %
176	148	6.8	149	2.7			6.8 - 2.7	4.1	6.8	100.0
177	140	11.3	148	6.8	<i>Pseudotragus parvidens</i>	8.1	11.3 - 6.8	4.5	3.2	71.1
178	147	2.4					2.4 - 0.0	2.4	2.4	100.0
179	147	2.4					2.4 - 0.0	2.4	2.4	100.0
180	142	11.1	147	2.4			11.1 - 2.4	8.7	11.1	100.0
181	146	1.8			<i>Hemitragus jayakari</i>	0.5	1.8 - 0.0	1.8	1.3	72.2
182	146	1.8					1.8 - 0.0	1.8	1.8	100.0
183	145	2.8	146	1.8	<i>Hemitragus orientalis</i>	2.8	2.8 - 1.8	1	0.0	0.0
184	145	2.8			<i>Hemitragus bonali</i>	0.5	2.8 - 0.0	2.8	2.3	82.1
185	143	8	145	2.8	<i>Tossunoria</i>	7	8.0 - 2.8	5.2	1.0	19.2
186	144	5.1					5.1 - 0.0	5.1	5.1	100.0
187	144	5.1					5.1 - 0.0	5.1	5.1	100.0
188	144	5.1					5.1 - 0.0	5.1	5.1	100.0
189	144	5.1			<i>Capra ibex</i>	1.3	5.1 - 0.0	5.1	3.8	74.5
190	144	5.1					5.1 - 0.0	5.1	5.1	100.0
191	144	5.1					5.1 - 0.0	5.1	5.1	100.0
192	144	5.1					5.1 - 0.0	5.1	5.1	100.0
193	144	5.1					5.1 - 0.0	5.1	5.1	100.0
194	144	5.1					5.1 - 0.0	5.1	5.1	100.0
195	143	8	144	5.1	<i>Norbertia hellenica</i>	5.4	8.0 - 5.1	2.9	2.6	89.7
196	142	11.1	143	8			11.1 - 8.0	3.1	11.1	100.0
197	141	11.1	142	11.1			11.1 - 11.1	0	11.1	0.0
198	141	11.1			<i>Ammotragus lervia</i>	0.1	11.1 - 0.0	11.1	11.0	99.1
199	140	11.3	141	11.1			11.3 - 11.1	0.2	11.3	100.0
200	139	14.5	140	11.3	<i>Pachytragus solignaci</i>	13.5	14.5 - 11.3	3.2	1.0	31.3
201	139	14.5			<i>Mesenbriacerus</i>	9.2	14.5 - 0.0	14.5	5.3	36.6
202	139	14.5			<i>Palaeoryx</i>	8.1	14.5 - 0.0	14.5	6.4	44.1
203	24	17.8	139	14.5			17.8 - 14.5	3.3	17.8	100.0
204	24	17.8			<i>Qurlignoris</i>	8.2	17.8 - 0.0	17.8	9.6	53.9
205	22	20.2	24	17.8			20.2 - 17.8	2.4	20.2	100.0
206	138	2.5			<i>Hippotragus leucophaeus</i>	0.6	2.5 - 0.0	2.5	1.9	76.0
207	138	2.5			<i>Hippotragus equinus</i>	2.5	2.5 - 0.0	2.5	0.0	0.0
208	137	8.8	138	2.5			8.8 - 2.5	6.3	8.8	100.0
209	137	8.8			<i>Hippotragus niger</i>	1.6	8.8 - 0.0	8.8	7.2	81.8
210	134	11	137	8.8			11.0 - 8.8	2.2	11.0	100.0

Branch #	Node Prior to Branch	Age of Previous Node	Node After Branch	Age of Node After Branch	Oldest Fossil	Age of Oldest Fossil	Time Interval Branch	Age of Lineage	Ghost Lineage Duration	Ghost Lineage %
211	136	2.5					2.5 - 0.0	2.5	2.5	100.0
212	136	2.5			<i>Oryx gazella</i>	2.5	2.5 - 0.0	2.5	0.0	0.0
213	136	2.5					2.5 - 0.0	2.5	2.5	100.0
214	135	5	136	2.5	<i>Oryx sp</i>	2.6	5.0 - 2.5	2.5	2.4	96.0
215	135	5					5.0 - 0.0	5	5.0	100.0
216	134	11	135	5	<i>"Predamalis" sp Damalacra</i>	7	11.0 - 5.0	6	4.0	66.7
217	23	17.9	134	11			17.9 - 11.0	6.9	17.9	100.0
218	133	6.2			<i>Damaliscus pygargus</i>	2	6.2 - 0.0	6.2	4.2	67.7
219	133	6.2			<i>Damaliscus lunatus</i>	0.6	6.2 - 0.0	6.2	5.6	90.3
220	132	7.7	133	6.2			7.7 - 6.2	1.5	7.7	100.0
221	132	7.7			<i>Damalacra neanica</i>	5.3	7.7 - 0.0	7.7	2.4	31.2
222	129	10.8	132	7.7			10.8 - 7.7	3.1	10.8	100.0
223	131	2.5			<i>Connochaetes taurinus</i>	2.5	2.5 - 0.0	2.5	0.0	0.0
224	131	2.5			<i>Connochaetes africanus</i>	1.6	2.5 - 0.0	2.5	0.9	36.0
225	129	10.8	131	2.5	<i>Connochaetes gentryi</i>	2.7	10.8 - 2.5	8.3	8.1	97.6
226	130	3.1			<i>Sigmoceros lichensteinii</i>	0.5	3.1 - 0.0	3.1	2.6	83.9
227	130	3.1			<i>Alcelaphus buselaphus</i>	0.6	3.1 - 0.0	3.1	2.5	80.6
228	129	10.8	130	3.1			10.8 - 3.1	7.7	10.8	100.0
229	23	17.9	129	10.8			17.9 - 10.8	7.1	17.9	100.0
230	22	20.2	23	17.9			20.2 - 17.9	2.3	20.2	100.0
231	21	22.3	22	20.2			22.3 - 20.2	2.1	22.3	100.0
232	21	22.3			<i>Aepyceros proemelampus</i>	7	22.3 - 0.0	22.3	15.3	68.6
233	16	23.2	21	22.3			23.2 - 22.3	0.9	23.2	100.0
234	128	1.6					1.6 - 0.0	1.6	1.6	100.0
235	128	1.6			<i>Kobus leche</i>	0.7	1.6 - 0.0	1.6	0.9	56.3
236	127	3.5	128	1.6			3.5 - 1.6	1.9	3.5	100.0
237	127	3.5			<i>Kobus ellipiprymnus</i>	2.33	3.5 - 0.0	3.5	1.2	33.4
238	125	3.5	127	3.5			3.5 - 3.5	0	3.5	0.0
239	126	1.2					1.2 - 0.0	1.2	1.2	100.0
240	126	1.2			<i>Kobus kob</i>	1.2	1.2 - 0.0	1.2	0.0	0.0
241	125	3.5	126	1.2			3.5 - 1.2	2.3	3.5	100.0
242	122	12.7	125	3.5	<i>Kobus presigmoidalis</i>	7	12.7 - 3.5	9.2	5.7	62.0
243	124	3			<i>Redunca redunca</i>	1.7	3.0 - 0.0	3	1.3	43.3
244	124	3			<i>Redunca arundinum</i>	1.8	3.0 - 0.0	3	1.2	40.0
245	123	6.7	124	3	<i>Redunca darti</i>	2.8	6.7 - 3.0	3.7	3.9	100.0

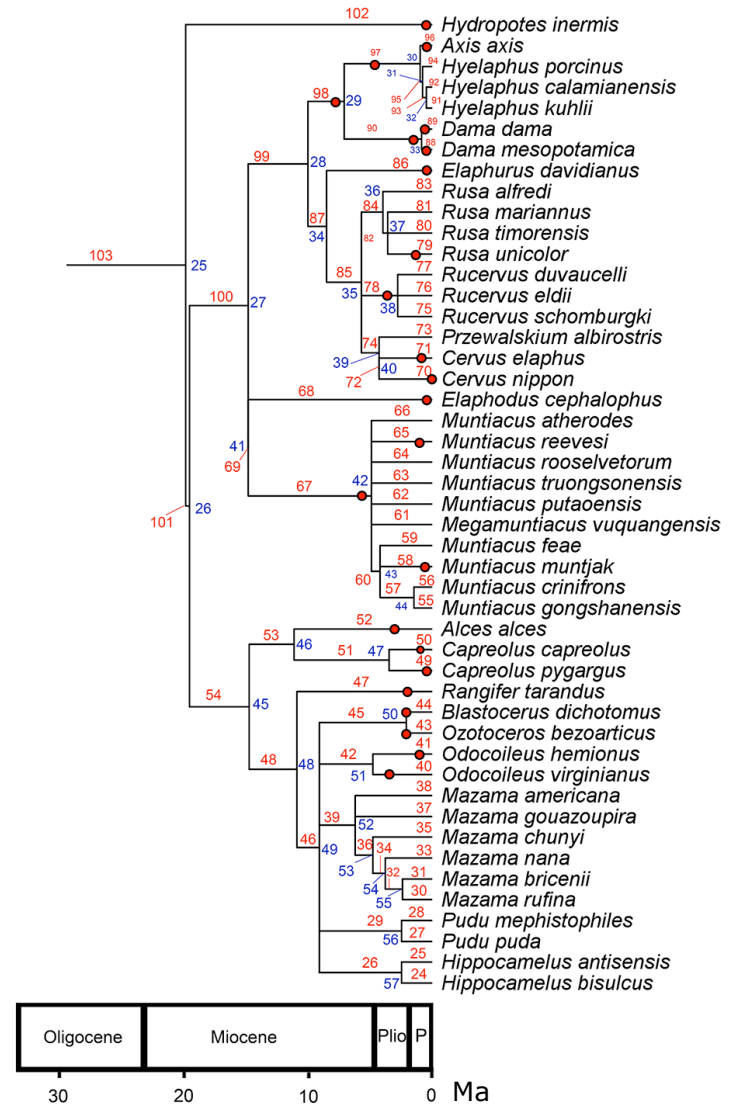
Branch #	Node Prior to Branch	Age of Previous Node	Node After Branch	Age of Node After Branch	Oldest Fossil	Age of Oldest Fossil	Time Interval Branch	Age of Lineage	Ghost Lineage Duration	Ghost Lineage %
246	123	6.7			<i>Redunca fulvorufula</i>	2.5	6.7 - 0.0	6.7	4.2	62.7
247	122	12.7	123	6.7			12.7 - 6.7	6	12.7	100.0
248	20	13.5	122	12.7			13.5 - 12.7	0.8	13.5	100.0
249	20	13.5			<i>Pelea sp</i>	5.3	13.5 - 0.0	13.5	8.2	60.7
250	19	19.8	20	13.5			19.8 - 13.5	6.3	19.8	100.0
251	121	5.1			<i>Philantomba monticola</i>	2.5	5.1 - 0.0	5.1	2.6	51.0
252	121	5.1					5.1 - 0.0	5.1	5.1	100.0
253	106	13.5	121	5.1			13.5 - 5.1	8.4	13.5	100.0
254	120	4.6					4.6 - 0.0	4.6	4.6	100.0
255	120	4.6					4.6 - 0.0	4.6	4.6	100.0
256	116	10	120	4.6			10.0 - 4.6	5.4	10.0	100.0
257	119	4.5					4.5 - 0.0	4.5	4.5	100.0
258	119	4.5					4.5 - 0.0	4.5	4.5	100.0
259	118	7.5	119	4.5			7.5 - 4.5	3	7.5	100.0
260	118	7.5					7.5 - 0.0	7.5	7.5	100.0
261	117	8.5	118	7.5			8.5 - 7.5	1	8.5	100.0
262	117	8.5					8.5 - 0.0	8.5	8.5	100.0
263	116	10	117	8.5			10.0 - 8.5	1.5	10.0	100.0
264	107	10.8	116	10			10.8 - 10.0	0.8	10.8	100.0
265	115	1.6					1.6 - 0.0	1.6	1.6	100.0
266	115	1.6					1.6 - 0.0	1.6	1.6	100.0
267	113	3.9	115	1.6			3.9 - 1.6	2.3	3.9	100.0
268	114	0.8					0.8 - 0.0	0.8	0.8	100.0
269	114	0.8					0.8 - 0.0	0.8	0.8	100.0
270	113	3.9	114	0.8			3.9 - 0.8	3.1	3.9	100.0
271	112	7.7	113	3.9			7.7 - 3.9	3.8	7.7	100.0
272	112	7.7					7.7 - 0.0	7.7	7.7	100.0
273	109	9.8	112	7.7			9.8 - 7.7	2.1	9.8	100.0
274	111	3.2					3.2 - 0.0	3.2	3.2	100.0
275	111	3.2					3.2 - 0.0	3.2	3.2	100.0
276	110	4.7	111	3.2			4.7 - 3.2	1.5	4.7	100.0
277	110	4.7					4.7 - 0.0	4.7	4.7	100.0
278	109	9.8	110	4.7			9.8 - 4.7	5.1	9.8	100.0
279	109	9.8					9.8 - 0.0	9.8	9.8	100.0
280	108	10.2	109	9.8			10.2 - 9.8	0.4	10.2	100.0

Branch #	Node Prior to Branch	Age of Previous Node	Node After Branch	Age of Node After Branch	Oldest Fossil	Age of Oldest Fossil	Time Interval Branch	Age of Lineage	Ghost Lineage Duration	Ghost Lineage %
281	108	10.2					10.2 - 0.0	10.2	10.2	100.0
282	107	10.8	108	10.2			10.8 - 10.2	0.6	10.8	100.0
283	106	13.5	107	10.8			13.5 - 10.8	2.7	13.5	100.0
284	105	13.5	106	13.5			13.5 - 13.5	0	13.5	0.0
285	105	13.5			<i>Sylvicapra gimnia</i>	0.1	13.5 - 0.0	13.5	13.4	99.3
286	19	19.8	105	13.5			19.8 - 13.5	6.3	19.8	100.0
287	16	23.2	19	19.8			23.2 - 19.8	3.4	23.2	100.0
288	104	7.9					7.9 - 0.0	7.9	7.9	100.0
289	104	7.9			<i>Raphicerus melanotis</i>	0.6	7.9 - 0.0	7.9	7.3	92.4
290	104	7.9			<i>Raphicerus campestris</i>	1.8	7.9 - 0.0	7.9	6.1	77.2
291	103	8.9	104	7.9			8.9 - 7.9	1	8.9	100.0
292	103	8.9					8.9 - 0.0	8.9	8.9	100.0
293	80	19.7	103	8.9			19.7 - 8.9	10.8	19.7	100.0
294	102	2.7					2.7 - 0.0	2.7	2.7	100.0
295	102	2.7					2.7 - 0.0	2.7	2.7	100.0
296	100	5.3	102	2.7			5.3 - 2.7	2.6	5.3	100.0
297	101	1.4					1.4 - 0.0	1.4	1.4	100.0
298	101	1.4					1.4 - 0.0	1.4	1.4	100.0
299	100	5.3	101	1.4			5.3 - 1.4	3.9	5.3	100.0
300	80	19.7	100	5.3	<i>Madoqua sp</i>	7	19.7 - 5.3	14.4	12.7	88.2
301	99	3.9					3.9 - 0.0	3.9	3.9	100.0
302	99	3.9					3.9 - 0.0	3.9	3.9	100.0
303	98	6.2	99	3.9			6.2 - 3.9	2.3	6.2	100.0
304	98	6.2					6.2 - 0.0	6.2	6.2	100.0
305	80	19.7	98	6.2	<i>Gazella schlosseri</i>	9.3	19.7 - 6.2	13.5	10.4	77.0
306	97	1.5			<i>Gazella tingitana</i>	0.1	1.5 - 0.0	1.5	1.4	93.3
307	97	1.5					1.5 - 0.0	1.5	1.5	100.0
308	97	1.5			<i>Gazella pomeli</i>	0.8	1.5 - 0.0	1.5	0.7	46.7
309	91	5.7	97	1.5	<i>Gazella borbonica</i>	3.8	5.7 - 1.5	4.2	1.9	45.2
310	96	0.8			<i>Gazella dorcas</i>	0.1	0.8 - 0.0	0.8	0.7	87.5
311	96	0.8					0.8 - 0.0	0.8	0.8	100.0
312	93	2.3	96	0.8			2.3 - 0.8	1.5	2.3	100.0
313	95	0			<i>Gazella gazella</i>	0.01	0.0 - 0.0	0	0.0	0.0
314	95	0			<i>Gazella arabica</i>	0.01	0.0 - 0.0	0	0.0	0.0
315	94	1.4	95	0			1.4 - 0.0	1.4	1.4	100.0

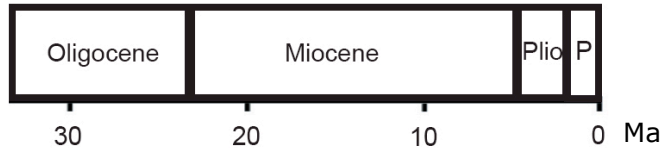
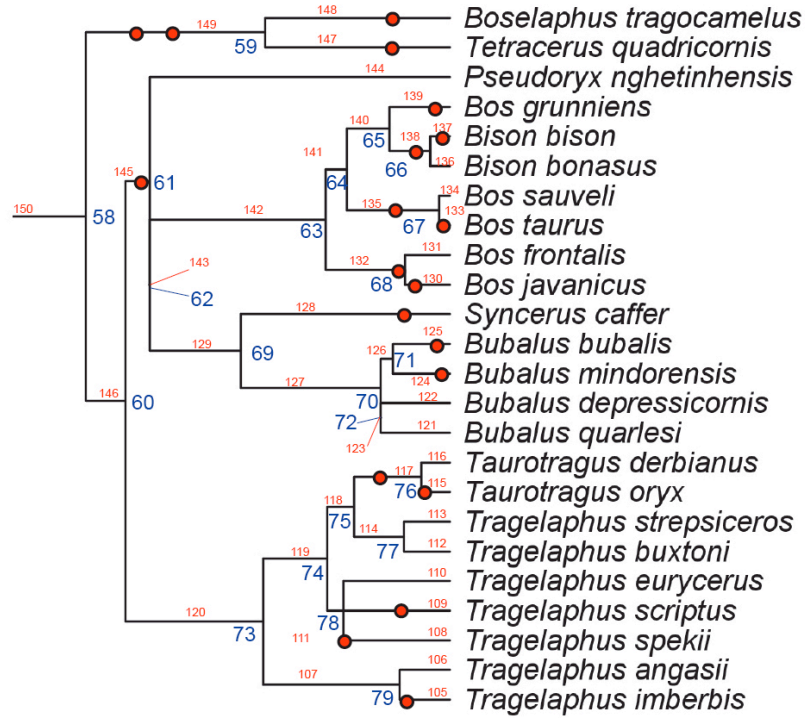
Branch #	Node Prior to Branch	Age of Previous Node	Node After Branch	Age of Node After Branch	Oldest Fossil	Age of Oldest Fossil	Time Interval Branch	Age of Lineage	Ghost Lineage Duration	Ghost Lineage %
316	94	1.4					1.4 - 0.0	1.4	1.4	100.0
317	93	2.3	94	1.4			2.3 - 1.4	0.9	2.3	100.0
318	93	2.3					2.3 - 0.0	2.3	2.3	100.0
319	92	2.5	93	2.3			2.5 - 2.3	0.2	2.5	100.0
320	92	2.5					2.5 - 0.0	2.5	2.5	100.0
321	91	5.7	92	2.5	<i>Gazella borbonica</i>	3.8	5.7 - 2.5	3.2	1.9	59.4
322	85	10.6	91	5.7	<i>Gazella deperdita</i>	8.6	10.6 - 5.7	4.9	2.0	40.8
323	90	3.1					3.1 - 0.0	3.1	3.1	100.0
324	90	3.1					3.1 - 0.0	3.1	3.1	100.0
325	89	4.4	90	3.1			4.4 - 3.1	1.3	4.4	100.0
326	89	4.4			<i>Nanger granti</i>	0.5	4.4 - 0.0	4.4	3.9	88.6
327	86	10.6	89	4.4	<i>Gazella sp</i>	5.3	10.6 - 4.4	6.2	5.3	85.5
328	88	1.9					1.9 - 0.0	1.9	1.9	100.0
329	88	1.9					1.9 - 0.0	1.9	1.9	100.0
330	87	4.8	88	1.9			4.8 - 1.9	2.9	4.8	100.0
331	87	4.8			<i>Eudorcas rufina</i>	0.1	4.8 - 0.0	4.8	4.7	97.9
332	86	10.6	87	4.8	<i>Gazella sp</i>	7	10.6 - 4.8	5.8	3.6	62.1
333	85	10.6	86	10.6			10.6 - 10.6	0	10.6	0.0
334	84	18	85	10.6	<i>Gazella nigerensis</i>	18	18.0 - 10.6	7.4	0.0	0.0
335	84	18			<i>Prostrepsiceros</i>	10.9	18.0 - 0.0	18	7.1	39.4
336	82	18	84	18			18.0 - 18.0	0	18.0	0.0
337	83	4.2			<i>Antidorcas recki</i>	2.6	4.2 - 0.0	4.2	1.6	38.1
338	83	4.2					4.2 - 0.0	4.2	4.2	100.0
339	82	18	83	4.2			18.0 - 4.2	13.8	18.0	100.0
340	82	18					18.0 - 0.0	18	18.0	100.0
341	81	18	82	18			18.0 - 18.0	0	18.0	0.0
342	81	18			<i>Saiga tatarica</i>	0.5	18.0 - 0.0	18	17.5	97.2
343	80	19.7	81	18			19.7 - 18.0	1.7	19.7	100.0
344	80	19.7			<i>Ourebia ourebi</i>	1.6	19.7 - 0.0	19.7	18.1	91.9
345	16	23.2	80	19.7			23.2 - 19.7	3.5	23.2	100.0
346	18	3.4					3.4 - 0.0	3.4	3.4	100.0
347	18	3.4					3.4 - 0.0	3.4	3.4	100.0
348	17	5.4	18	3.4			5.4 - 3.4	2	5.4	100.0
349	17	5.4					5.4 - 0.0	5.4	5.4	100.0
350	16	23.2	17	5.4			23.2 - 5.4	17.8	23.2	100.0
351	16	23.2			<i>Oreotragus major</i>	3.2	23.2 - 0.0	23.2	20.0	86.2
352	15	25.4	16	23.2			25.4 - 23.2	2.2	25.4	100.0
353	8	32	15	25.4	<i>Hanhaicerus qii</i>	29	32.0 - 25.4	6.6	3.0	45.5
354	5	33.2	8	32			33.2 - 32.0	1.2	33.2	100.0
355	1	50	5	33.2	<i>Archaeomeryx</i>	49	50.0 - 33.2	16.8	1.0	6.0
356			1	50	<i>Pseudamphimeryx</i>	53.3	0.0 - 50.0	-50	-53.3	100.0



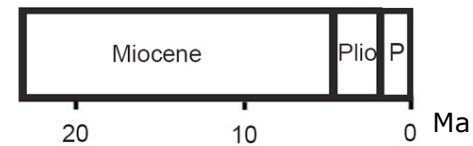
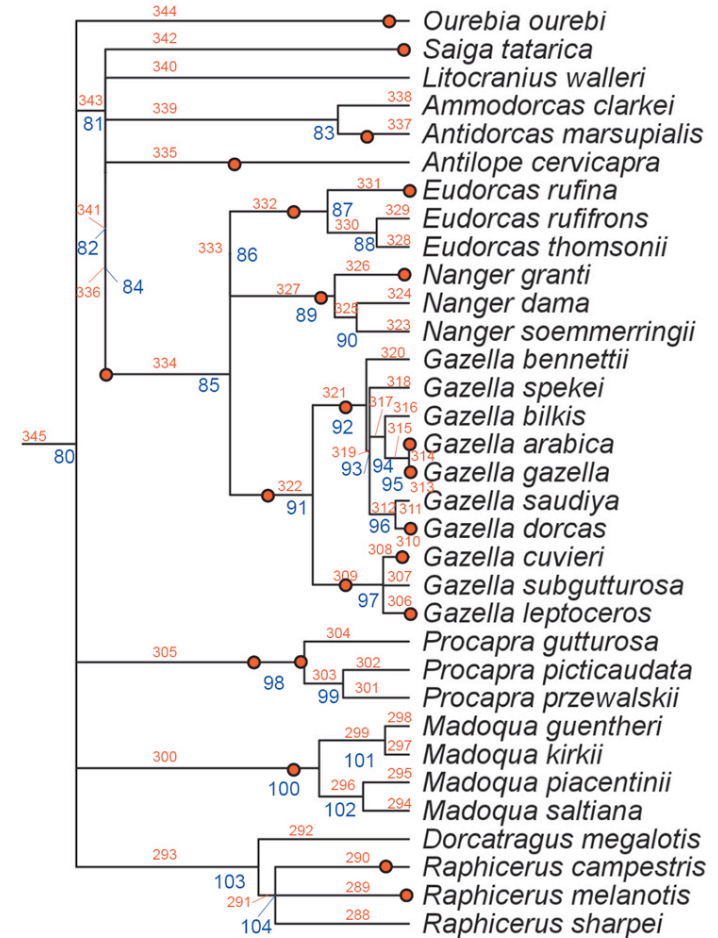
Appendix 2.A. Phylogeny of Ruminantia (Hernández Fernández & Vrba 2005a) showing the main subfamilies and Tragulidae, Giraffidae and Moschidae. Red spots, oldest fossil record for each branch. Numbers of nodes and branches match those in Appendix I. Red Numbers, number of branches. Blue Numbers, numbers of nodes.



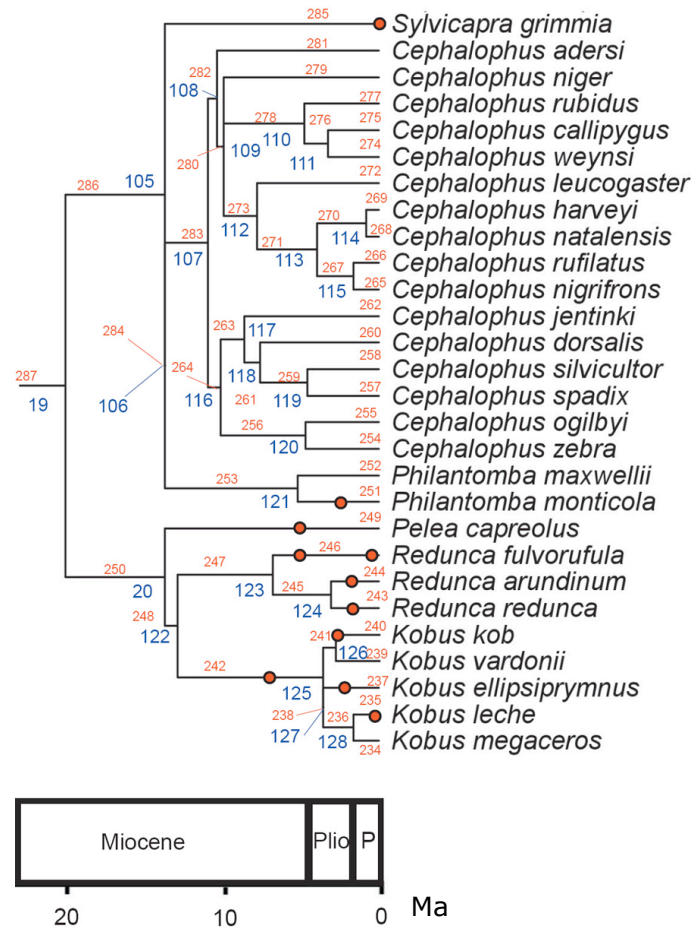
Appendix 2.B. Phylogeny of Cervidae (Hernández Fernández & Vrba 2005a). Legend as in Appendix 2.A.



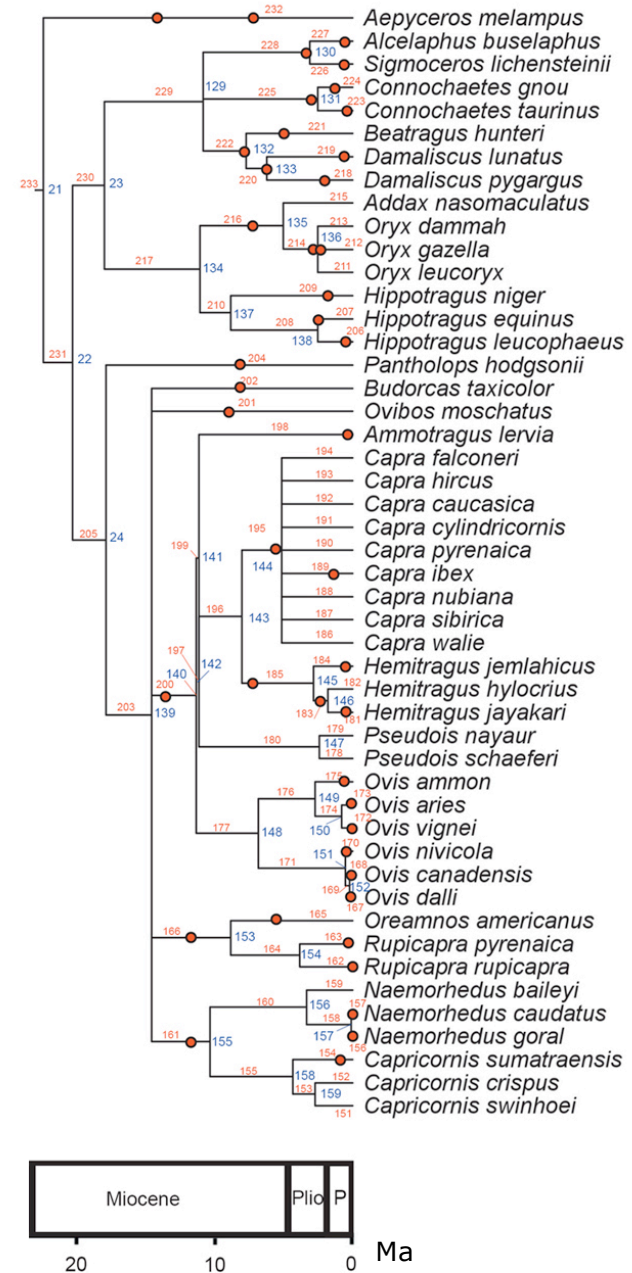
Appendix 2.C. Phylogeny of Bovinae (Hernández Fernández & Vrba 2005a). Legend as in Appendix 2.A.



Appendix 2.D. Phylogeny of Antilopinae (Hernández Fernández & Vrba 2005a). Legend as in Appendix Appendix 2.A.



Appendix 2.E. Phylogeny of Cephalophinae, Peleinae and Reduncinae (Hernández Fernández & Vrba 2005a). Legend as in Appendix 2.A.



Appendix 2.F. Phylogeny of Aepycerotinae, Alcelophinae, Hippotraginae, Pantholopinae and Caprinae (Hernández Fernández & Vrba 2005a). Legend as in Appendix 2.A.