

## ORIGINAL ARTICLE

# Species longevity in North American fossil mammals

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## Abstract

Species longevity in the fossil record is related to many paleoecological variables and is important to macroevolutionary studies, yet there are very few reliable data on average species durations in Cenozoic fossil mammals. Many of the online databases (such as the Paleobiology Database) use only genera of North American Cenozoic mammals and there are severe problems because key groups (e.g. camels, oreodonts, pronghorns and proboscideans) have no reliable updated taxonomy, with many invalid genera and species and/or many undescribed genera and species. Most of the published datasets yield species duration estimates of approximately 2.3–4.3 Myr for larger mammals, with small mammals tending to have shorter species durations. My own compilation of all the valid species durations in families with updated taxonomy (39 families, containing 431 genera and 998 species, averaging 2.3 species per genus) yields a mean duration of 3.21 Myr for larger mammals. This breaks down to 4.10–4.39 Myr for artiodactyls, 3.14–3.31 Myr for perissodactyls and 2.63–2.95 Myr for carnivorous mammals (carnivorans plus creodonts). These averages are based on a much larger, more robust dataset than most previous estimates, so they should be more reliable for any studies that need species longevity to be accurately estimated.

**Key words:** Cenozoic, genus, mammals, North America, species

## INTRODUCTION

The topic of species longevity has long been of interest to paleontologists (see summary in Hopkins 2011). The duration of species through geologic time has been related to geographic range, body size, reproductive rates, extinction probabilities, niche variation, intrapopulation variation, speciation rates and many other evolutionary

and extinction-related characteristics. Stanley (1975, 1979, 1981) uses species longevity in mammals *versus* bivalves as one of his tests of the ‘species selection’ model of evolution.

However, the comparison of species longevity to other variables is often hampered by the problem of outdated or flawed species-level taxonomy in many groups. In some cases, there is no recent reliable species-level taxonomy any other paleontologist can use, so comparison to other ecological and evolutionary variables is impossible. Nevertheless, paleontologists have tried to make such comparisons, using genera instead of species, in databases such as FAUNMAP, MIOMAP, NEOMAP, as well as the Paleobiology Database (PBDB). Using gen-

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era as a proxy for species is done as a matter of necessity and by default, but there are many biologists and paleontologists who argue that the species is the only biologically natural unit in the biota and regard genera as relatively poor proxies for true species diversity (see review of the topic in Cracraft 1989).

It is well known that there are many higher-level taxa (e.g. the families of fossil mammals) that have not been revised recently but potentially will undergo big changes in total species and generic diversity. Once they are revised, the use of largely invalid generic data on these poorly known groups is 'garbage in, garbage out'. This is particularly a problem with North American Cenozoic mammals, where some groups are grossly oversplit and have no valid taxonomy available but were used in the compilation of MIOMAP and PBDB nevertheless. Unlike the database of Eurasian Cenozoic mammals, which has been continuously revised for many years by a variety of paleontologists, the North American mammalian database is still full of invalid and outdated taxonomy that hampers efforts to look at species-level processes or to conduct analyses on the species level.

This anomaly is due to several factors. First, the incredible Frick Collection of fossil mammals in the American Museum of Natural History remained virtually unstudied until the 1970s (and is only now being slowly published piecemeal). That collection is so immense, with so many more complete and well-documented fossils, that it forced a complete revision of every group of Mid and Late Cenozoic mammals on the continent. In many cases, a major group remained virtually unstudied for decades until work on the Frick Collection produced a monographic burst (e.g. Wang 1994; Wang *et al.* 1999; Tedford *et al.* 2009, on canids; my own work on rhinocerotids in 2005). In addition, many fossil mammalian families were burdened with the work of taxonomists who are widely considered incompetent, from Frick's 1937 ruminant monograph, to the Schultz and Falkenbach (1968) oreodont monograph, to Osborn's brontothere monograph (1929) and proboscidean monograph (1936). Although some of these works have since been revised (e.g. Muhlbachler's 2008 brontothere monograph replaces Osborn 1929), many others have not (e.g. there is still no updated taxonomy on proboscideans, oreodonts, pronghorns or many of Frick's ruminants). In the Frick Collection alone, there is an entire floor of fossil camels and another floor of proboscideans that are virtually unstudied. I have personally experienced this problem with the current outdated state of the taxonomy of camels (see Prothero 1996a; Honey *et al.*

1998), oreodonts (see Stevens & Stevens 1996; Prothero & Sanchez 2008), antilocaprids (see Janis & Manning 1998) and peccaries (Wright 1998; Prothero 2009; D. R. Prothero, unpubl. data).

These and many other important groups make up a significant part of many Cenozoic faunas and my own experience has taught me that their published taxonomy is so bad as to be positively misleading. I have personally revised other important Miocene groups, such as the Rhinocerotidae (Prothero 2005), the dromomerycine palaeomerycids (Prothero & Lister 2008), the blastomerycine musk deer (Prothero 2008) and the protoceratids (Prothero 1998b), and documented the effects of the outdated taxonomy on the generic databases now available. For the example, the PBDB recognizes only 7 North American fossil genera of peccaries but Wright's (1998) revision suggests that there are a large number of undescribed and unnamed genera, and my revision (D. R. Prothero, unpubl. data) recognizes at least 18 genera. In contrast, Prothero and Lister (2008) found that one-third of the dromomerycid genera and half of the species in the PBDB were invalid. Thus, the generic-level databases can severely overestimate or underestimate the true number of taxa if the compilers have not kept up with these rapid taxonomic changes. Those who use the PBDB for Neogene mammals may not fully appreciate the inherent flaws in calculating generic diversity based on bad taxonomy.

Rather than accept generic longevity as a proxy for the evolutionary trends in species through time, it is worthwhile reviewing the published literature for areas where the taxonomy of a large group (such as Cenozoic mammals) is well studied with widely accepted, up-to-date species taxonomy and examining whether the true longevity of species shows any consistent patterns within and between taxa and whether generic longevity data correlate well with species durations.

## MATERIALS AND METHODS

Species longevity for Cenozoic fossil mammals were compiled from the published literature and from large datasets from a number of sources. For the within-family approach, I extracted longevity of species as reported in the most recent revision of a group (cited below), modified as necessary when I was aware of problematic taxa. The time scale of the species ranges follows the individual chapters in Woodburne (2004), as modified in Janis *et al.* (1998, 2008). The time duration of each species was tabulated from their actual biostra-

tigraphic range using range-through methods. As much as possible, I used the chronostratigraphic dating of the actual documented stratigraphic first and last occurrence data for each species, rather than lumping them into coarser-resolution bins of ‘land mammal ages’. I did not extend ranges using inferred ghost lineages because the cladistic relationships in some families are too poorly known to do this reliably. Generic ranges were calculated from the oldest and youngest known members of valid species and do not reflect incomplete specimens that could not be identified to species but might extend the generic range (in contrast to the methods used by Janis *et al.* 1998, 2008). I did not use any extant species to avoid the ‘pull of the recent’ effect and any isolated stem-group taxa not assignable to a monophyletic crown group at the family level. For reasons of space, I focused on the larger carnivorous and herbivorous mammalian groups (primarily Carnivora, Artiodactyla and Perissodactyla) so that the Eurasian–African NOW database (the NOW database: <http://www.helsinki.fi/science/now/>) and North American databases are comparable. Small mammal groups are certainly worth examining, although their species-level taxonomy in North America is still in flux and adding all of them was beyond the scope of the present study. Thus, among North American mammals I did not count the following

large mammal groups whose species-level taxonomy is still insufficiently studied: Camelidae, Antilocapridae, oreodonts, primitive carnivorans (‘Miacidae’), Xenarthra and the Proboscidea. All the rest of the families listed below have sufficiently updated taxonomy (cited below). I entered the raw data into an Excel spreadsheet and then calculated the statistics. Histograms were plotted using StatPlus LE.

## RESULTS

Two approaches can be taken to looking at fossil species longevity in fossil mammals: a broad faunal survey approach (all the named taxa in a temporal interval that has been well studied and has a stable species-level taxonomy) or a phylogenetic within-family approach (all of the species within a particular family-level group that has undergone recent systematic revision).

### Faunal surveys

Although an up-to-date, modern species taxonomic database is not available for all Cenozoic mammal faunas, there are some time and geographic intervals that have undergone thorough revision. For example, the large number of paleontologists who have studied Pleistocene mammals in both the Old World and the

**Table 1** Estimates of species durations in Cenozoic mammals from different regions and different data sources

Region	Age	Mean duration (Myr)	Source
Europe	Pleistocene	1.0	Kurtén 1968
Europe	Neogene	2.2 (large mammals)	Liow <i>et al.</i> 2008
Europe	Neogene	2.4 (small mammals)	Liow <i>et al.</i> 2008
Europe–Africa	Neogene	6.3 (large mammals)	Raia <i>et al.</i> 2012
Europe–Africa	Neogene	4.8 (large mammals)	Raia <i>et al.</i> 2012
Europe–Africa	Neogene	3.7 (large mammals)	NOW database
Africa	Neogene	2.3 (large mammals)	Vrba 2000
Asia	Neogene	2.5 (artiodactyls)	Flynn <i>et al.</i> 1995
North America	Eocene	2.6	Stanley 1978, 1979
North America	Eocene	0.8–1.0	Gingerich 1980, 1985
North America	Oligocene	2.37	Prothero & Heaton 1996
North America	Cenozoic	3.21 (large mammals)	This study (raw data)
North America	Cenozoic	3.21 (large mammals)	This study (family averages)
North America	Cenozoic	4.39 (artiodactyls)	This study (raw data)
North America	Cenozoic	4.10 (artiodactyls)	This study (family averages)
North America	Cenozoic	3.14 (perissodactyls)	This study (raw data)
North America	Cenozoic	3.31 (perissodactyls)	This study (family averages)
North America	Cenozoic	2.95 (carnivores)	This study (raw data)
North America	Cenozoic	2.63 (carnivores)	This study (family averages)

New World allows such summaries. Kurtén (1968) published one of the first such estimates (Table 1) and gave a mean duration for most Pleistocene mammal species of the Old World as approximately 1 Myr; this figure was cited by Stanley (1975, 1979) for use in comparison with rates of evolution in other groups, such as bivalves. Liow *et al.* (2008) look at more recent data for Neogene mammals of the Old World (the NOW database: <http://www.helsinki.fi/science/now/>) and find that small mammal genera and species have longer median durations than large mammal genera. In Table S1 of the Supplementary Data Series 1 of Liow *et al.* (2008), a mean duration of all large mammal species of 2.17 Myr is calculated, with a median duration of 1.5 Myr (1106 species total). For small mammal species ( $n = 868$ ), the mean was 2.4 Myr and the median value was 1.5 Myr.

Raia *et al.* (2012) also analyze the NOW database, focusing on just 72 species of ungulates, carnivores and proboscideans with good fossil records in Europe and Africa. I extracted the raw data from their Table S1 in the electronic supplementary material available online. In that data table, they quote 2 different sets of statistics: 'Duration' is 'stratigraphic distribution in millions of years'; and 'FA' and 'LA' are last appearance datums. I cannot determine why it is that when I calculated 'FA–LA' that it does not match 'Duration' of the species in millions of years, so the results were calculated separately. The 'Duration' column produces a mean value of 6.29 Myr and a median value of 4.76 Myr, while subtracting 'FA–LA' produces a mean value of 4.8 Myr and a median of 3.5 Myr. P. Raia (pers. comm.) provided me with the spreadsheet of their original compilation of the NOW dataset, with 555 species of European and African mammals. This dataset gives a mean of 3.739 Myr for all of these species combined.

Flynn *et al.* (1995) use the large chronostratigraphically-controlled dataset of Miocene–Pliocene mammals from the Siwalik Hills of Pakistan to compile species durations in southern Asia. They find a mean duration of 1.3 Myr for the rodents and 2.5 Myr for the artiodactyls, but do not average or plot the data from other orders (perissodactyls, proboscideans) because of the small sample size.

Vrba (2000) and Vrba and DeGusta (2004) estimate the average species duration of larger African mammals at 2.33 Myr. Their original data are not available for analysis, so it was not possible to calculate the median, or to break this number down into taxonomic or ecological categories, but it is considerably shorter than the

durations estimated by Raia *et al.* (2012) for some of the same taxa.

Estimates of species durations in North American mammals are less common. Stanley (1978, 1979) quotes a mean duration of Eocene mammal species at 2.6 Myr, but Gingerich (1980, 1985) gives durations of 0.8–1.0 Myr for species from the Early Eocene of the Bighorn Basin, Wyoming. Prothero and Heaton (1996) survey the durations of all the known species from the upper Eocene–Oligocene White River Group in the High Plains. They find a mean duration of 2.37 Myr for 177 species, with very long durations for insectivores (6.7 Myr) and carnivorous mammals (4.6 Myr) and very short durations for rodents (1.14 Myr) and lagomorphs (1.58 Myr), with hoofed mammals (artiodactyls = 2.91 Myr; perissodactyls = 2.20 Myr) coming in between. These numbers are consistent with those of Flynn *et al.* (1995), who find rodents tend to have shorter mean species durations than those of larger mammals, such as artiodactyls.

The data discussed above are summarized in Table 1. Even though the estimates of mean species duration are not identical, most of the datasets produce mean species duration of approximately 2–3 Myr, with only a handful of outliers that are significantly shorter or longer. The trend for carnivorous mammals to have the longest ranges in the Eocene–Oligocene of North America (Prothero & Heaton 1996) is not upheld by the trends observed in the NOW database of Europe and Africa in the Neogene (Table 2).

**Table 2** Comparison of durations (in Myr) of species within the same order between the Neogene of the Old World (OW), from the NOW database, after Raia *et al.* (2012) and the Paleogene (Late Eocene–Oligocene) of the North America (NAO) (Prothero & Heaton 1996) and the Cenozoic of North America (NAC) (this study)

Taxon	Species	Duration	<i>N</i> (spp.)
Carnivorous mammals	OW	4.6	14
	NAO	4.6	32
	NAC	2.9	366
Perissodactyls	OW	7.1	18
	NAO	2.2	29
	NAC	3.1	209
Artiodactyls	OW	5.6	34
	NAO	2.9	41
	NAC	4.4	150

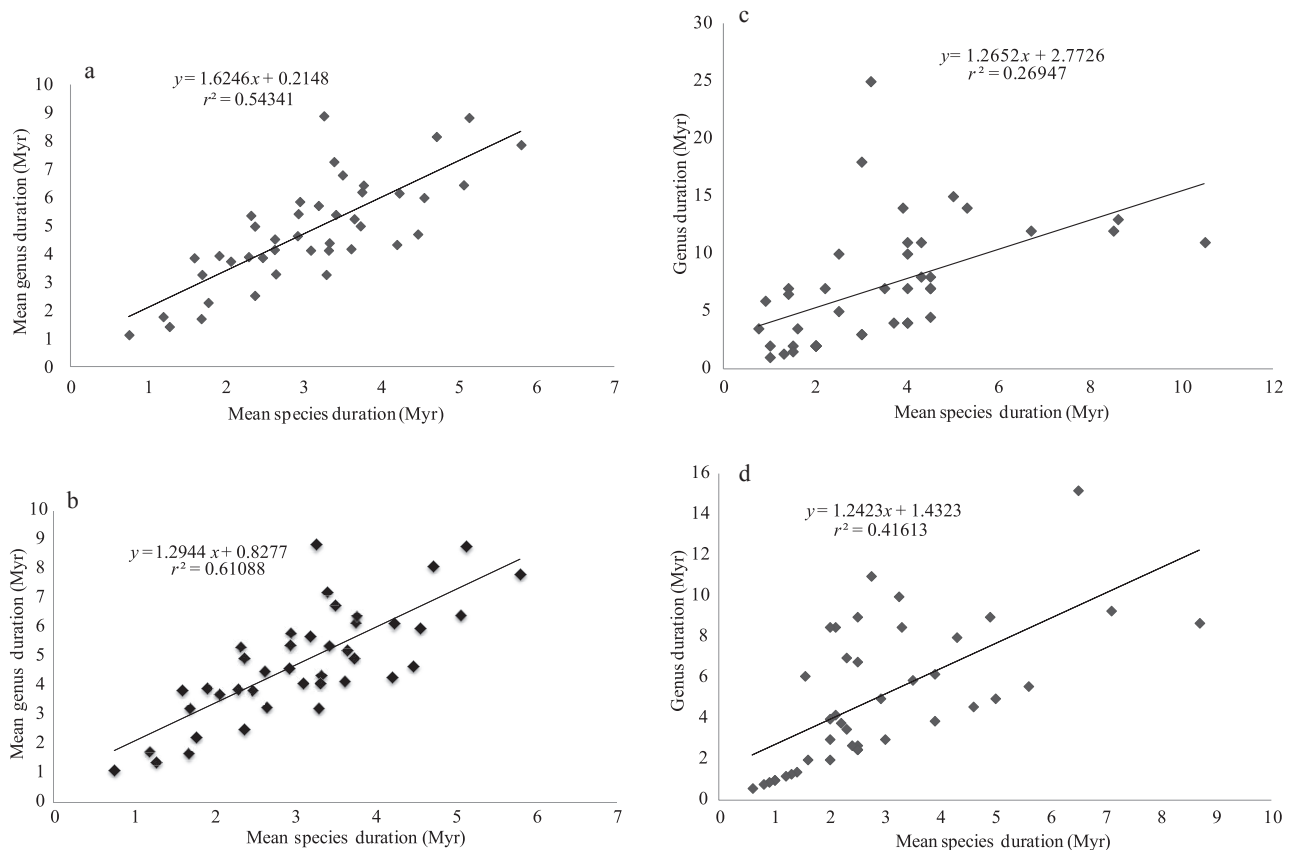
### Within-family species durations

As described in the Materials and Methods section, I compiled all the temporal ranges for all the valid species and genera within North American mammalian families with valid, updated taxonomy. Results are shown in Table 3 and Figure 1. A total of 39 mammalian families were tabulated, containing 431 genera and 998 species, which averages approximately 2.3 species per genus. Mean durations for species in these genera averaged by family (Table 3) ranged from 0.75 Myr (Pantolambdidae) to 6.58 Myr (Hypertragulidae). The mean for all artiodactyl species was 3.96 Myr; for perissodactyls, 3.31 Myr; and for carnivores, 2.63 Myr. The combined mean duration of all 983 species was 3.19 Myr. Slightly different values were obtained when all the raw species duration data within an order were averaged independent of fam-

ily. The mean for all large mammals was 3.21 Myr (virtually the same as obtained by averaging family means). The mean for artiodactyls was 4.39 Myr (compared to 3.96 Myr from averaging family means). The mean for perissodactyls was 3.14 Myr (compared to 3.31 Myr by averaging family means). Finally, the mean for carnivorous mammals was 2.95 Myr (compared to 2.63 Myr obtained by averaging family means).

These numbers are all within the range of values quoted in earlier studies (Table 1), although they show carnivores with shorter durations than ungulates, the opposite of what Prothero and Heaton (1996) find for the mammals of the Eocene–Oligocene White River Fauna.

Figure 1 shows a least-squares regression of the relationship between mean species duration and mean generic duration. Clearly, the 2 variables are moderately well



**Figure 1** Least-squares regression of the relationship between mean species duration and mean generic duration in each of the 85 mammalian families in this study. (a) Entire dataset. (b) Dataset excluding the 3 outliers (Tapiridae, Hypertragulidae, Leptomerycidae), resulting in a somewhat stronger correlation. In both plots, the line is the least-squares fit and the lower limit is the lower threshold of 1 genus per species (all monospecific genera). (c) Regression of average number of species per genus in the Canidae. (d) Same as c, but for the Equidae. In both plots c and d, the monospecific genera form a clear trend line along the lower threshold of the dataset.



**Table 3** Summary of data of valid species and genera in each family of North American mammals

Family	<i>N</i> spp.	<i>N</i> genera	Avg.sp.dur.	Avg.gen.dur	Source
Artiodactyla					
Anthracotheriidae	15	6	2.32	5.4	Kron & Manning 1998
Helohyidae	10	5	3.33	4.4	Stucky 1998
Entelodontidae	15	6	5.13	8.83	Effinger 1998
Tayassuidae	26	17	3.32	4.14	Wright 1998; Prothero 2009; D. R. Prothero, unpubl. data
Protoceratidae	30	13	4.23	6.16	Prothero 1998b
Oromerycidae	9	6	4.55	6	Prothero 1998a
Leptomerycidae	11	4	4.72	13	Webb 1998
Hypertragulidae	12	5	6.58	14.2	Webb 1998
Moschidae	9	6	4.71	8.16	Prothero 2008
Palaeomerycidae	16	12	4.47	4.71	Prothero & Liter 2008
Leptochoeridae	10	5	3.09	4.14	Stucky 1998
Antiacodontidae	9	5	2.37	2.54	Stucky 1998
Homacodontidae	16	11	2.64	3.3	Stucky 1998
Artiodactyla mean	14.46	7.77	3.96	6.53	
Perissodactyla					
Chalicotheriidae	8	4	3.73	5.00	Coombs 1998
Amynodontidae	8	5	3.75	6.20	Wall 1998
Hyracodontidae	13	5	3.50	6.80	Prothero 1996b, 1998c
Rhinocerotidae	37	16	3.77	6.44	Prothero 1998d, 2005
Tapiridae	14	6	2.60	11.22	Colbert & Schoch 1998
Isectolophidae	8	3	2.93	5.43	Colbert & Schoch 1998
Brontotheriidae	27	21	3.29	3.28	Mihlbachler 2008
Equidae	121	37	2.92	4.65	Froehlich 2002; Hulbert 1993; MacFadden 1998; Prothero and Shubin 1989
Perissodactyla mean	29.50	12.13	3.31	6.13	
Carnivorous mammals					
Canidae	135	39	3.39	7.27	Wang 1994; Wang <i>et al.</i> 1999; Tedford <i>et al.</i> 2009
Felidae	24	11	2.29	3.91	Martin 1998
Nimravidae	15	7	2.95	5.86	Bryant 1996
Ursidae	23	17	1.77	2.29	Hunt 1998b
Amphicyonidae	34	12	3.19	5.72	Hunt 1998a
Procyonidae	19	11	2.06	3.75	Baskin 1998b
Mustelidae	55	38	3.61	4.19	Baskin 1998a
Oxyaenidae	27	10	1.91	3.95	Gunnell 1998
Hyaendontidae	35	15	2.47	3.88	Gunnell 1998
Carnivore mean	40.78	17.78	2.63	4.54	
Miscellaneous families					
Conoryctidae	7	5	1.27	1.44	Lucas <i>et al.</i> 1998
Stylinodontidae	7	4	5.8	7.87	Lucas <i>et al.</i> 1998
Esthonychidae	8	5	4.2	4.34	Lucas & Schoch 1998b
Pantolambdidae	6	2	0.75	1.15	Lucas 1998
Barylambdidae	7	4	1.68	1.72	Lucas 1998
Uintatheriidae	6	4	5.06	6.45	Lucas & Schoch 1998a
Arctocyonidae	50	15	1.59	3.87	Archibald 1998
Hyopsodontidae	35	8	2.37	4.99	Archibald 1998
Mioclaenidae	26	9	1.69	3.28	Archibald 1998
Periptychiidae	35	13	1.19	1.79	Archibald 1998
Phenacodontidae	20	4	3.26	8.89	Archibald 1998
Miscellaneous mean	18.82	6.64	2.62	4.16	
Combined means	24.61	10.65	3.19	5.40	

*N* spp., number of species in family; *N* genera, number of genera in family; Avg.sp.dur, average species duration (in Myr); Avg.gen.dur, average genus duration (in Myr).

correlated by the standards of paleoecological datasets such as these data. The  $r^2 = 0.54$  for the entire dataset is considerably better ( $r^2 = 0.61$ ) if the 3 outliers (Hypertragulidae, Leptomerycidae and Tapiridae) are excluded (Fig. 1b). (For some reason, those 3 families have a lot of anomalously long-lived species.) Note in the plots in Figure 1a and b that although there are several outliers above the least-squares lines (i.e. genera with unusually long average durations relative to their average species longevity), there cannot be similar outliers below the line. That is because there is a lower threshold in the field below the least-squares line, because it is impossible for a species to have a duration longer than the genus to which it belongs. Thus, the lower limit for the data would be a line where the number of species and genera are exactly equal (i.e. each genus is monospecific and monotypic).

One reviewer suggested that the correlation might improve if the durations of genera and average species duration in a given family were plotted against each other. To test this hypothesis, I chose 2 of the largest families (to improve sample size and, thus, the likelihood of a higher  $r^2$  value), the Canidae and Equidae. In fact, the opposite is the case: the correlation was much poorer when examined at the genus *versus* species level (Fig. 1c,d). Least-squares lines fitted to these plots give  $r^2$  values of 0.2–0.4. The reason for this much poorer correlation is apparent when the plot is examined in detail. At the within-family level, there are a number of genera that are monospecific (genus and species range are identical), producing an obvious trend of points lined along the bottom of the scatter. The least-squares line is trying to fit the overall scatter of points when there are actually 2 trends: the 1:1 line of monospecific genera and the cluster of the rest of the taxa plotted above that threshold. However, the plots of durations at the family level (Fig. 1a,b) contain no monotypic groups, because averaging genera and species durations prevents this from occurring (all families had at least 2 genera and more than 2 species). Consequently, the trend line fits a lot better.

## DISCUSSION

The compilation of raw species longevity data, based on a new taxonomy of North American large mammals, provides a number of results consistent with previous studies and others that differ remarkably from the published literature.

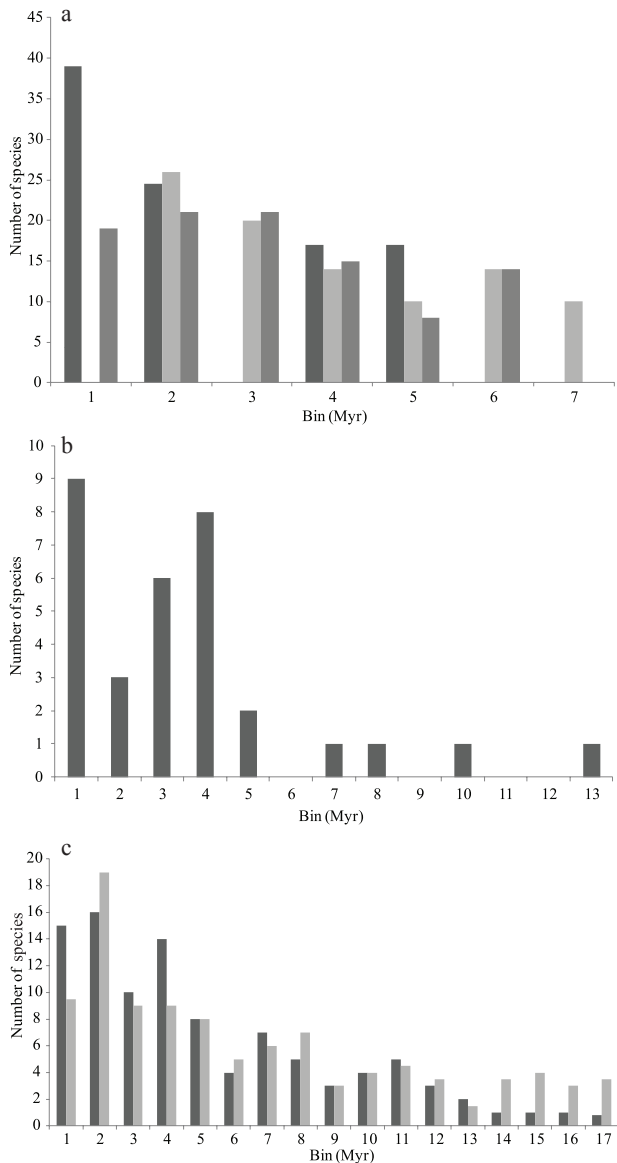
Species durations of fossil mammals as estimated by a number of different methods (Table 1) provide rough-

ly similar results, with most datasets giving mean species durations of approximately 2–4 Myr. Thus, the 1-Myr average duration for European Pleistocene mammals reported by Kurtén (1968) is an underestimate determined before the rigorous work in dating and taxonomy of the past 40 years (see more recent estimates in the NOW database).

Some datasets (e.g. Flynn *et al.* 1985; Prothero & Heaton 1996) suggest that small mammals have shorter species durations than do large mammals, although others (e.g. Raia *et al.* 2012) indicate the opposite. With the existence of the large dataset summarized in this study, it should be possible to see whether or not this trend holds true when the small mammal species are compiled and analyzed.

Most comparisons of species durations are done with histograms, such as those seen in analyses by Liow *et al.* (2008) and Flynn *et al.* (1995). Figure 2a shows histograms of the 3 major ordinal-level groups of large mammals in this study: artiodactyls, perissodactyls and carnivorous mammals (Carnivora plus Creodonta). All 3 plots are slightly skewed toward a greater representation of the shorter-lived taxa, but not strongly so. By contrast, in their study of Neogene Siwalik mammals, Flynn *et al.* (1995; see Fig. 2b) show a distribution of artiodactyls that is strongly skewed toward shorter-lived species and also contains some very long-lived species. Some are longer in duration than most of the species in my dataset. Liow *et al.* (2008) analyze the Neogene mammals of Eurasia and Africa and produce an even more strongly skewed histogram for both large and small-bodied mammals, with a very high percentage of the species in the very short-ranging (less than 1 Myr) categories. Their histogram (see Fig. 2c) also includes numerous species with durations longer than 15 Myr, something that is completely lacking in my dataset.

The lack of updated species-level taxonomy in North American fossil mammals has been a hindrance to efforts to use existing databases (e.g. PBDB, NEOMAP, MIOMAP and FAUNMAP) that only contain genera. Without species-level data, it is difficult to analyze these data to solve other interesting paleontological problems. To get around this problem, some (e.g. Alroy 2002) have proposed statistical models to estimate the number of valid species knowing the number of genera. The present study provides empirical evidence of how many species and genera are actually considered valid as of the latest taxonomic revisions. Thus, if we know that there are  $x$  number of genera in the dataset, our empirical data suggests that there should be  $2.3x$  valid species (because,



**Figure 2** Distribution of total number of species of a given longevity. Each bin represents the proportion of the total species lasting between 0 and 1 Myr, 1 and 2 Myr, and so on. (a) Data from the North American Cenozoic. The left-hand dark bar is the carnivorous mammals, the middle gray bar is artiodactyls, and the right-hand dark bar is perissodactyls. (b) Artiodactyls from the Neogene of the Siwalik Hills, Pakistan (replotted from Flynn *et al.* 1995, fig. 3). (c) Data from the Neogene of the Old World database (NOW) (replotted from Liow *et al.* 2008, fig. 1). The dark bar is large mammals, the gray bar is small mammals. Note that the North American data set is much more evenly distributed, with not nearly as high a proportion of short-ranging species (except in the carnivores), and does not range to species with durations greater than 9 Myr.

as demonstrated above, each genus has, on average, 2.3 species in the dataset).

## CONCLUSIONS

Many different estimates of the average duration of fossil mammal species have been provided over the past 50 years. Most give mean durations in the order of 2–4 Myr, although there are some time intervals (e.g. the Early Eocene) that are alleged to have shorter durations of species. Comparison of the existing datasets for larger mammals of the Old World (both carnivorous mammals and prey, such as artiodactyls and perissodactyls) and North America (this study) reveals broadly similar results, although the North American mammals do not have such a high proportion of short-lived species, nor are there as many species with durations as long as 15 Myr or longer.

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