Live long and prosper? assessing longevity of small mammal taxa using the NOW database

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Chapter 8
Live Long and Prosper? Assessing Longevity of Small Mammal Taxa Using the NOW Database

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Abstract Extinction is part of life. Some groups persist longer than others, as is confirmed in an analysis of the small mammal data in the NOW database. Longevities are shorter in Rodentia than in Eulipotyphla and Lagomorpha. At the family level, the shortest longevities both for genera and species lies with the most diverse groups, whereas families with low diversity tend to have a longer duration of their representatives. This suggests that competition between phylogenetically related species creates Red Queen dynamics that lead to a shorter duration of (chrono)-species in the more diverse groups, whereas taxa that have little competition can persist for a much longer time.

Keywords Competition • Diversity • Eulipotyphla • Extinction • Lagomorpha • Rodentia

Introduction

All life ends. Just as this holds true for individuals, so every species on Earth sooner or later will face extinction. And just as each species has its own life expectancy, so does the species duration differ between different groups. Mammals are known to have a shorter species duration than invertebrates (e.g., Stanley, 1975) and also within mammals differences in longevity have been recorded between groups. Flynn et al. (1995), for instance, recorded for the Siwaliks a median duration of rodent species of 1.3 my (million years), whereas the same value for artiodactyls of the region was 2.4–2.5 my. By contrast, Liow et al. (2008) found at the genus level for the Neogene of Europe somewhat longer median durations for small mammals than for large mammals (2.4 my vs. 2.2 my, respectively) and a higher origination and extinction rate for the latter. Prothero (2014) found a longer median value for the large mammals of the Cenozoic of North America (3.21 my) with different values for the artiodactyls (4.9 my), perissodactyls (3.14 my) and carnivores (2.95 my). Raia et al. (2012) found a median value of 4.5 my for large mammal taxa of Europe and Africa, selected for their good fossil record. Prothero (2014) recalculated that value with a considerably shorter outcome (3.5 my).

Smits (2015) used the North American fossil mammal record to model which biological traits could be of influence on species duration. He found a significant phylogenetic and temporal effect. A phylogenetic component is in line with the different median durations that Flynn et al. (1995) and Prothero (2014) found for different groups of mammals. Notably, the temporal effect found suggested a larger extinction risk for Paleogene mammals than for Neogene groups. This is in agreement with the observation of Flynn et al. (1995) who found shorter species durations in the Paleogene of Wyoming than for the Neogene Siwalik record. These authors noted that the Middle Miocene part of their record represented a period of environmental stability (Flynn et al., 1995; Mahmood Raza, 1983). Such stability would promote longer durations for species living at the time, whereas periods of faunal turnover will be a time of increased extinctions.

The small mammal record of the Neogene basins in northeastern Spain includes the same time range as the Siwalik record and is another example of a long term record that can be used to show periods of stability and episodes of faunal turnover. Using the origination and extinction events of this record, Van Dam et al. (2006) found a pattern of regularity in the frequency of peaks, which could be correlated with astronomical nodes. A number of these peaks coincided with known faunal turnover events. One of these

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peaks showed a cyclicity of ~2.4 my, which is in the same order of magnitude as the median mammal species durations cited in literature (e.g., Alroy, 2000; Vrba & De Gusta, 2004). As the peaks can also be linked to climatic perturbations, environmental stability is definitely a factor in the extinction risk of mammalian taxa. It is equally clear that, whereas the median duration of mammal species lies around 2.5 my, many species remain unaltered for longer periods, unaffected by events that spell the end for other taxa (e.g., *Armantomys aragoniensis*, *Galerix exilis*). And, as we noted, there seems to be a phylogenetic component that favors some groups to have longer survival periods.

Whereas for large mammals species durations have been compared between different groups (Prothero, 2014), studies involving small mammals have lumped them as a single grouping (Liow et al., 2008) or discussed rodents only (Flynn et al., 1995). In this chapter, we use data from the NOW database to explore patterns of longevity of both genera and species in three orders of small mammals: Rodentia, Eulipotyphla and Lagomorpha. Judging from the strong preference for rodents and more specifically murids in biochronological schemes, we anticipate that the rodents will have shorter durations than the insectivores and lagomorphs. Particularly the insectivores have often been cited as a group with relatively little evolutionary change (e.g., Furió et al., 2015). To our knowledge, this is the first study that compares longevity at the family level. This way we aim to see whether the phylogenetic signal found for high-level taxonomic groups, with different longevities for different orders, is mirrored at lower taxonomic levels. Small mammals are particularly suited for such a study, as the three mammalian orders considered here together already comprise 49% of the extant fauna, based on Burgin et al. (2018), and have, certainly in Europe, an excellent fossil record.

Material and Methods

Datasets for the Rodentia, Eulipotyphla and Lagomorpha were downloaded separately from the NOW database in February 2020 (The NOW Community, 2021). Any taxonomic issues we encountered during our analyses were corrected both in the dataset and in the NOW database. In order to facilitate comparison between different regions, we recorded for each taxon the continent(s) in which it occurred based on the countries as recorded in the database. We considered Europe and Asia as separate entities, but, because of its geographic position, included the Anatolian record with the former.

For each genus the first and last occurrences were sought manually. Occurrences that were not identified at the species level were not taken into account, because they represent a larger uncertainty of the identification. Locality ages in the NOW database are given with a minimum and maximum age, usually based on a time-unit (e.g., NALMA, MN unit, magnetostratigraphic chron), sometimes in combination with a radiometric age. First and last occurrences of taxa were calculated by taking the average of the minimum and maximum age of the first and last time units in which a taxon occurred. In the case of overlapping time units, we opted for the one with the shortest duration. The longevity of each genus was subsequently calculated by subtracting the age of the last occurrence from that of the first occurrence. Eccentric occurrences, creating a major gap in the stratigraphic distribution of a taxon, were considered suspicious and removed from the analysis.

The procedure for calculating longevities for genera was repeated for species. We only calculated the longevity for species that had at least five occurrences in the database. Calculating longevities using the average age of time units is a relatively coarse tool. However, given that a correlation to a time unit is the most precise dating for the vast majority of localities, it maximizes the number of taxa across the database for which age data can be extracted.

Statistics were done with the software environment R (v.4.0.2) (R Development Core Team, 2020). The packages "ggplot2" and "ggExtra" are used for graphic representation. Only families with more than five species (for species longevity) or genera (for genus longevity) are represented in boxplots. Simple linear regressions are plotted with a 95% confidence interval. Regression equations are provided in Appendix 8.1. The data for all families are listed in Tables 8.1 and 8.2. Similar data are also provided for Muridae subfamilies in Table 8.3. Potential outliers are detected with the Interquartile range (IQR) criterion. Family outliers are listed in Appendix 8.2. Finally, the geographic distribution of the genera whose duration have been calculated are provided in Appendix 8.3, with the number of included species.

Results

Our dataset comprises 19,750 species occurrences for the Rodentia, 5,991 for Eulipotyphla and 2,185 for Lagomorpha. Longevity durations were calculated for 826 rodent genera, 237 eulipotyphlan genera and 65 genera of lagomorphs. Because of the way we calculated the ranges of taxa, a duration of 0 my is found for all genera that have records from one period only. This was the case for 318 rodent, 95 eulipotyphlan and 22 lagomorph genera. Notably, this includes 77 out of the 87 South American rodents, which is not surprising as the South American record in the NOW database is still in the early phases of development. Species durations were calculated for species that had at

Table 8.1 Descriptive statistics of species and genus longevity in Rodentia families. Species with a range of 0 and/or less than 5 occurrences are not considered

Taxa	Species-level					Genus-level				
	Mean	Median	0–100%	sd	N	Mean	Median	0–100%	Sd	n
Rodentia										
Anomaluridae	2.18	2.70	1.15–2.70	0.89	3	3.50	3.50	1.37–5.63	3.01	2
Aplodontidae	4.23	3.35	1.55–7.80	3.22	3	6.70	5.40	1.35–19.20	5.17	15
Bathyergidae	3.19	3.19	2.70–3.68	0.69	2	2.74	2.70	1.76–3.89	0.77	5
Bathyergoididae	1.40	1.41	–	–	1	2.70	2.70	–	–	1
Castoridae	6.29	5.23	1.50–15.33	4.22	24	8.13	7.48	1.50–16.10	4.43	24
Caviidae	–	–	–	–	–	5.80	5.80	5.35–6.25	0.64	2
Chinchillidae	–	–	–	–	–	3.43	3.43	2.35–4.50	1.52	2
Ctenodactylidae	3.79	3.79	1.90–5.68	2.67	2	4.97	4.78	0.80–8.33	2.64	6
Cylindrodontidae	3.09	2.55	1.40–4.80	1.42	5	3.78	2.88	2.40–7.20	1.89	6
Dasyproctidae	–	–	–	–	–	4.50	4.50	–	–	1
Diamantomyidae	4.83	4.83	–	–	1	3.91	3.91	–	–	1
Diatomyidae	–	–	–	–	–	1.50	1.50	–	–	1
Dinomyidae	–	–	–	–	–	6.55	6.55	4.10–9.00	3.46	2
Dipodidae	4.13	3.05	0.75–13.65	3.76	16	5.28	3.08	0.60–19.22	4.90	24
Distylomyidae	–	–	–	–	–	14.11	14.12	–	–	1
Eomyidae	3.85	2.19	0.29–15.40	3.64	30	5.21	3.98	0.78–15.40	4.57	28
Erethizontidae	–	–	–	–	–	2.35	2.33	–	–	1
Eutypomyidae	3.20	3.20	–	–	1	5.50	3.08	2.90–12.95	4.97	4
Florentiamyidae	–	–	–	–	–	8.20	8.85	4.20–10.90	2.96	4
Geomyidae	4.19	1.50	0.83–9.90	4.43	6	5.34	3.50	0.85–16.75	5.26	9
Geomyoidea	3.43	3.43	2.35–4.50	1.52	2	6.08	3.17	1.00–21.55	7.77	6
Gerbillidae	0.51	0.51	–	–	1	–	–	–	–	–
Gliridae	4.64	3.80	0.10–12.58	2.95	84	9.10	7.43	0.90–25.10	6.89	30
Griphomyidae	4.80	4.80	–	–	1	2.85	2.85	0.90–4.80	2.76	2
Heliscomyidae	2.63	2.63	1.05–4.20	2.23	2	11.20	11.20	–	–	1
Heteromyidae	4.59	3.20	1.50–13.05	3.85	11	8.19	7.60	1.50–15.30	4.56	13
Hydrochaeridae	0.83	0.83	–	–	1	4.03	4.03	–	–	1
Hystricidae	2.28	1.54	0.72–4.98	1.56	8	6.47	6.47	4.76–8.19	2.42	2
Ischyromyidae	4.53	4.35	0.15–12.1	2.92	27	9.54	9.30	1.40–25.90	6.67	17
Jimonyidae	–	–	–	–	–	9.95	9.95	4.50–1540	7.71	2
Kenyamyidae	1.55	1.55	–	–	1	2.70	2.70	2.70–2.70	0.00	2
Muridae	2.35	1.90	0.03–9.85	1.75	309	3.65	2.72	0.21–14.85	2.84	204
Mylagaulidae	6.84	7.35	2.75–9.90	3.13	4	6.20	7.05	1.00–9.90	3.27	13
Myophiomyidae	3.99	3.99	2.70–5.28	1.82	2	3.99	3.99	2.70–5.26	1.82	2
Octodontidae	–	–	–	–	–	2.35	2.35	–	–	1
Pedetidae	4.20	4.20	–	–	1	3.26	1.76	1.25–6.78	3.06	3
Phiomyidae	–	–	–	–	–	2.93	3.00	0.70–5.00	2.03	4
Protoptychidae	–	–	–	–	–	1.75	1.75	–	–	1
Pseudosciuridae	–	–	–	–	–	4.26	4.26	–	–	1
Sciuravidae	3.22	3.40	2.85–3.40	0.32	3	4.30	4.15	1.35–8.05	2.29	6
Sciuridae	4.43	3.08	0.80–14.90	3.43	54	8.88	7.66	0.55–20.11	5.97	42
Theridomyidae	–	–	–	–	–	4.94	3.98	1.61–9.52	2.88	9
Thryonomyidae	3.20	3.45	0.13–5.75	2.39	4	4.72	2.70	1.25–12.51	4.69	5
Total	3.38	2.53	0.03–15.33	2.84	609	5.49	4.03	0.21–25.90	4.69	507

least five occurrences in the database. This was the case for 680 rodent species, 187 eulipotyphlans and 74 lagomorphs.

Plotting species duration against occurrences provides a first impression of the dataset (Figs. 8.1, 8.2 and 8.3). Overall, there is a positive correlation between the number of occurrences and longevity. This was to be expected. With a higher number of occurrences, we are more likely to capture the real first and last occurrences of that taxon. Conversely, a species with a longer longevity offers a greater chance of being found in the fossil record, resulting in more

Table 8.2 Descriptive statistics of species and genus longevity in Lagomorpha and Eulipotyphla families. Species with a range of 0 and/or less than 5 occurrences are not considered

Taxa	Species-level					Genus-level				
	Mean	Median	0–100%	sd	n	Mean	Median	0–100%	sd	n
Lagomorpha										
Leporidae	4.04	3.10	1.55–11.67	2.74	36	6.48	3.48	0.40–19.92	5.86	23
Ochotonidae	3.94	3.28	0.60–12.15	2.63	33	7.16	6.44	0.16–20.20	5.30	22
Total	3.99	3.25	0.60–12.15	2.67	69	6.82	5.75	0.16–20.20	5.54	45
Eulipotyphla										
Aethomyloidae	9.19	9.19	–	–	1	9.19	9.19	–	–	1
Apternodontidae	2.68	2.36	1.28–4.40	1.58	3	5.75	5.75	–	–	1
Dimylidae	4.80	3.79	1.21–8.55	3.07	5	6.66	7.40	1.75–10.10	3.71	5
Erinaceidae	3.74	4.01	1.17–7.30	1.61	36	7.37	7.24	0.41–18.50	4.66	22
Geolabdidae	6.87	6.62	0.50–16.30	4.85	8	17.14	13.61	3.45–34.36	15.76	3
Heterosoricidae	4.59	4.40	3.80–5.55	0.71	7	9.66	10.85	2.72–18.68	1.70	7
Leipsanolestidae	0.17	0.17	–	–	1	2.67	2.67	–	–	1
Litocheridae	3.69	3.95	0.69–5.71	1.56	8	6.40	4.42	2.87–15.32	5.05	5
Micropternodontidae	2.45	2.45	1.01–3.90	2.04	2	2.40	2.40	0.90 – 3.90	2.12	2
Nyctitheriidae	5.10	5.31	3.94–5.87	0.87	4	7.00	6.07	0.82 – 15.32	5.59	6
Oligoryctidae	3.73	3.73	3.06–4.39	0.94	2	6.45	6.45	–	–	1
Plesiosoricidae	4.09	4.35	1.70–5.95	1.97	4	11.85	11.85	–	–	1
Proscalopidae	8.97	7.85	2.67–16.38	6.92	3	10.59	12.14	4.60–15.03	5.38	3
Sespedectidae	5.83	5.98	2.60–8.33	2.24	6	8.22	6.68	2.59–17.18	5.22	6
Soricidae	3.55	3.18	0.36–9.00	1.97	47	4.71	3.95	0.36–15.33	3.41	47
Talpidae	3.75	3.05	0.29–14.40	2.80	43	7.46	5.91	0.72–23.40	6.36	36
Total	4.05	3.85	0.17–16.38	2.59	181	6.72	5.15	0. 02–34.36	5.48	149

occurrences. However, this relationship is certainly not evident in species with few (<30) occurrences. In fact, some the longest longevities are found in species with only few occurrences (e.g., *Neatocastor hesperus*, 14.7 my, six occurrences; *Centetodon magnus*, 16.6 my, ten occurrences).

Comparing the North American and European records, as indicated by different symbols in Figs. 8.1, 8.2 and 8.3, the American record stands out by having far fewer occurrences per taxon. In part, this can be attributed to the American record comprising a number of composite localities (Fortelius et al., 2023), reducing the number of individual occurrences. Despite the lower number of occurrences, the American record shows many long-lived taxa. This is also apparent in the regression line, which is much steeper for the North American record than for the other regions. This suggests that the American micromammal record may have some taxonomic issues, mirroring the problems that Prothero (2014) noted when calculating longevities for the large mammal records of the continent. In addition, problems relating to the dating of localities may also play a role. For instance, we ignored the Late Miocene occurrences of *Promimomys* in the American record based on the controversial *Promimomys* date (e.g., Martin, 2010). However, we did not correct the dates for the other small mammals in these early *Promimomys* faunas.

A comparison of the longevities of the three small mammal orders as a whole (Fig. 8.4) shows that the distributions are skewed, with the median lying towards the short durations, but, particularly in the rodents and eulipotyphlans, also with some rare, very long durations. This is in line with the results from earlier mammal longevity studies (e.g., Liow et al., 2008; Prothero, 2014), where shorter durations were also found to be far more common. The Rodentia have the shortest median durations both for species (2.53 my) and for genera (4.03 my). This is not surprising, given that the order is by far the most diversified mammalian order. It also agrees with the rodents being very much at the center of small mammal biostratigraphy. The two other orders show longevities similar to one another. Eulipotyphla have a somewhat shorter median duration of genera than the Lagomorpha (5.15 my vs. 5.75 my), but a longer median duration at the species level (3.85 my vs. 3.25 my).

Looking at the boxplots for rodents and eulipotyphlans at the family level (Figs. 8.5A, 8.6 and 8.7), the spread of the median longevity between rodent families is between 2.72–9.30 my and for eulipotyphlans between 3.95–10.85 my.

Among rodents, the shortest median durations are found in the Muridae and the Soricidae, notably the most diverse families of their respective orders. However, the boxplots were constructed for families with at least five genera and

Table 8.3 Descriptive statistics of species and genus longevity in Muridae subfamilies. Species with a range of 0 and/or less than 5 occurrences are not considered

Taxa	Mean	Median	0–100%	sd	Number of genera	Number of species
Muridae						
Adelomyarioninae	0.42	–	–	–	1	1
Afrocricetodontinae	2.82	2.70	2.70–3.05	0.20	3	5
Anomalomyinae	9.01	9.01	6.38–11.65	3.73	2	12
Arvicolinae	1.75	1.50	0.21–4.79	1.01	45	242
Copemyinae	6.46	6.00	3.28–10.05	2.90	6	57
Cricetinae	4.30	4.14	0.35–8.60	2.60	18	91
Cricetodontinae	4.45	2.50	1.50–10.33	3.54	10	67
Cricetopsinae	5.68	5.68	5.55–5.80	0.18	2	8
Dendromurinae	10.48	10.48	10.48–10.49	0.01	2	11
Deomyinae	2.80	2.80	2.67–2.93	0.18		3
Eucricetodontinae	9.11	7.80	3.50–14.85	5.07	5	35
Eumyarioninae	9.25	9.25	5.55–12.95	5.23	2	13
Eumyinae	3.50	3.50	1.85–5.15	2.33	2	10
Gerbilinae	3.15	2.40	1.09–7.46	2.28	9	38
Lophiomyinae	0.55	–	–	–	1	2
Megacricetodontinae	5.28	5.28	1.90–8.65	4.77	2	33
Melissiodontinae	6.33	–	–	–	1	5
Microtoscoptinae	1.48	1.39	1.10–1.95	0.43	3	6
Murinae	3.17	3.00	0.37–7.02	1.77	45	219
Myocricetodontinae	4.48	3.24	1.93–12.20	3.87	6	27
Myospalacinae	3.09	1.18	1.15–8.88	3.85	4	25
Neotominae	3.87	3.94	1.50–7.35	2.67	6	42
Nesomyinae	4.10	3.76	2.67–6.22	1.50	4	9
Otomyinae	3.89	–	–	–	1	5
Platacanthomyinae	4.85	6.33	0.90–7.32	3.45	3	8
Pseudocricetodontinae	9.80	–	–	–	1	3
Rhizomyinae	3.97	2.94	1.35–7.85	2.56	8	26
Sigmodontinae	4.05	4.14	1.50–6.85	1.90	6	28
Spalacinae	5.17	5.65	4.06–5.80	0.96	3	17
Tachyoryctoidinae	2.38	–	–	–	1	2

both in the rodents and the eulipotyphlans there are families with shorter longevities (Tables 8.1 and 8.2). This concerns, however, taxa with few data points in the database and the short durations are therefore considered an artefact. On the other side of the spectrum, the longest durations for the rodents are found in the monotypic families Heliscomyidae (11.20 my) and Distylomyidae (14.12 my). For the eulipotyphlans, the longest durations also lie with families with low diversity, viz. the Geolabididae (13.61 my), the Proscalopidae (12.14 my) and the monotypic Plesiosoricidae (11.85 my). Notably, whereas the rodent family with the highest diversity has the shortest median duration, the second and third-most diverse families, respectively the Sciuridae and the Gliridae, are among the families with the longest durations for genera (7.66 my and 7.43 my, respectively).

The Muridae stand out in being by far the most diverse family, comprising 204 out of 507 genera in our analysis. This is partly because NOW uses a wide concept for the classification of the Muridae. The classification of this group is quite controversial and alternative classifications recognize taxonomic groups such as Spalacinae or Cricetinae as families of their own. As such, it is useful to also consider the longevities of subfamilies within the Muridae. Figure 8.5B gives boxplots for genus longevity among the subfamilies as recognized in the database. The shortest median longevity is found for the Arvicolinae (1.50 my). Apart from being, together with the Murinae, the most diverse subfamily with 45 genera, the voles are also the youngest split-off of the murid tree, originating around the beginning of the Pliocene. The short longevity is probably an artifact related to the high number of extant genera in the

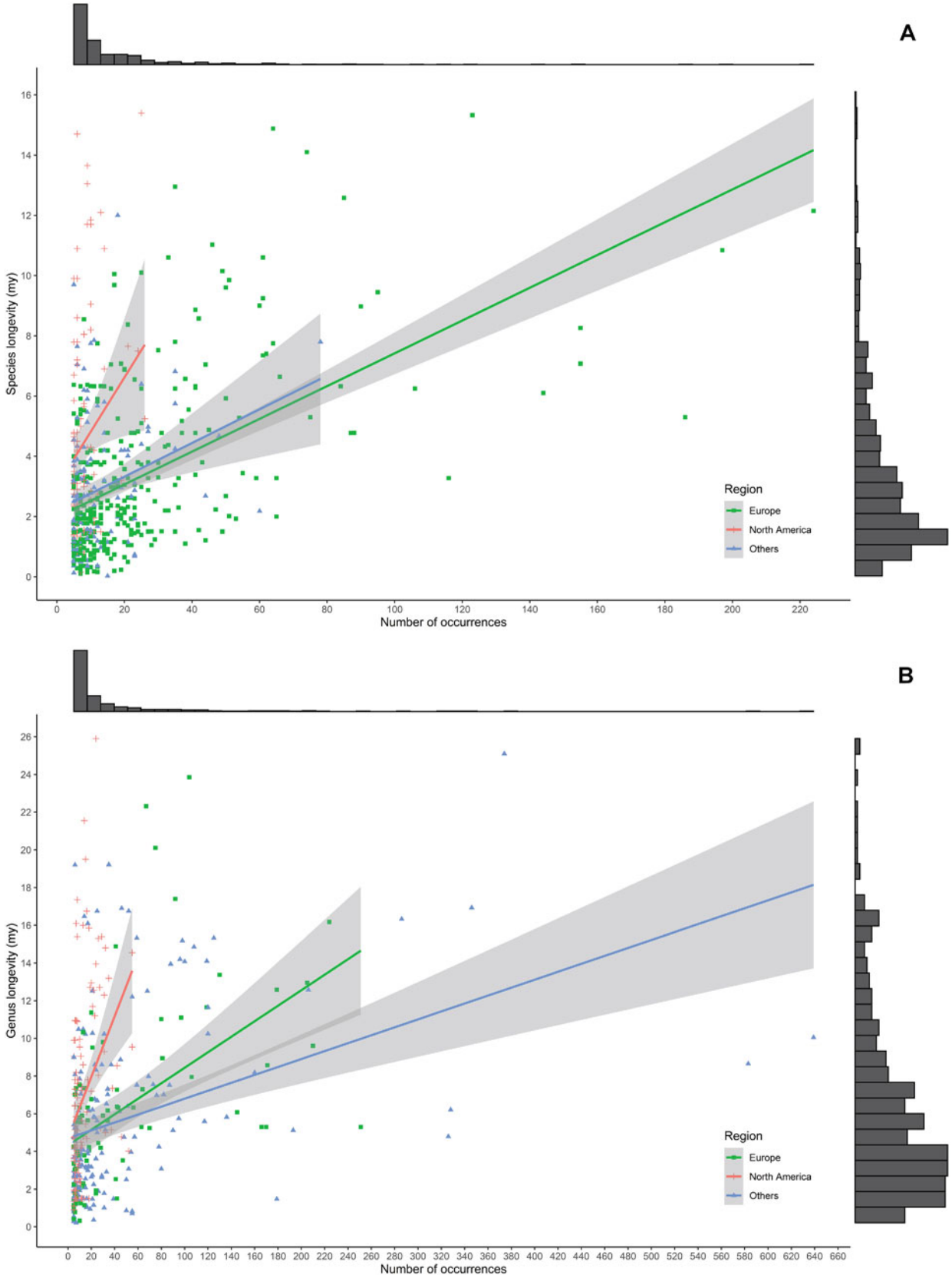

Fig. 8.1 Relation between the number of occurrences and the longevity of rodents, with marginal representation of distribution, for species longevity **A** and genus longevity **B**. European species are represented by green squares, North-American species by red crosses, and species from elsewhere by blue triangles. Species and genera with a range of 0 are not considered. Equations are provided in Appendix 8.1

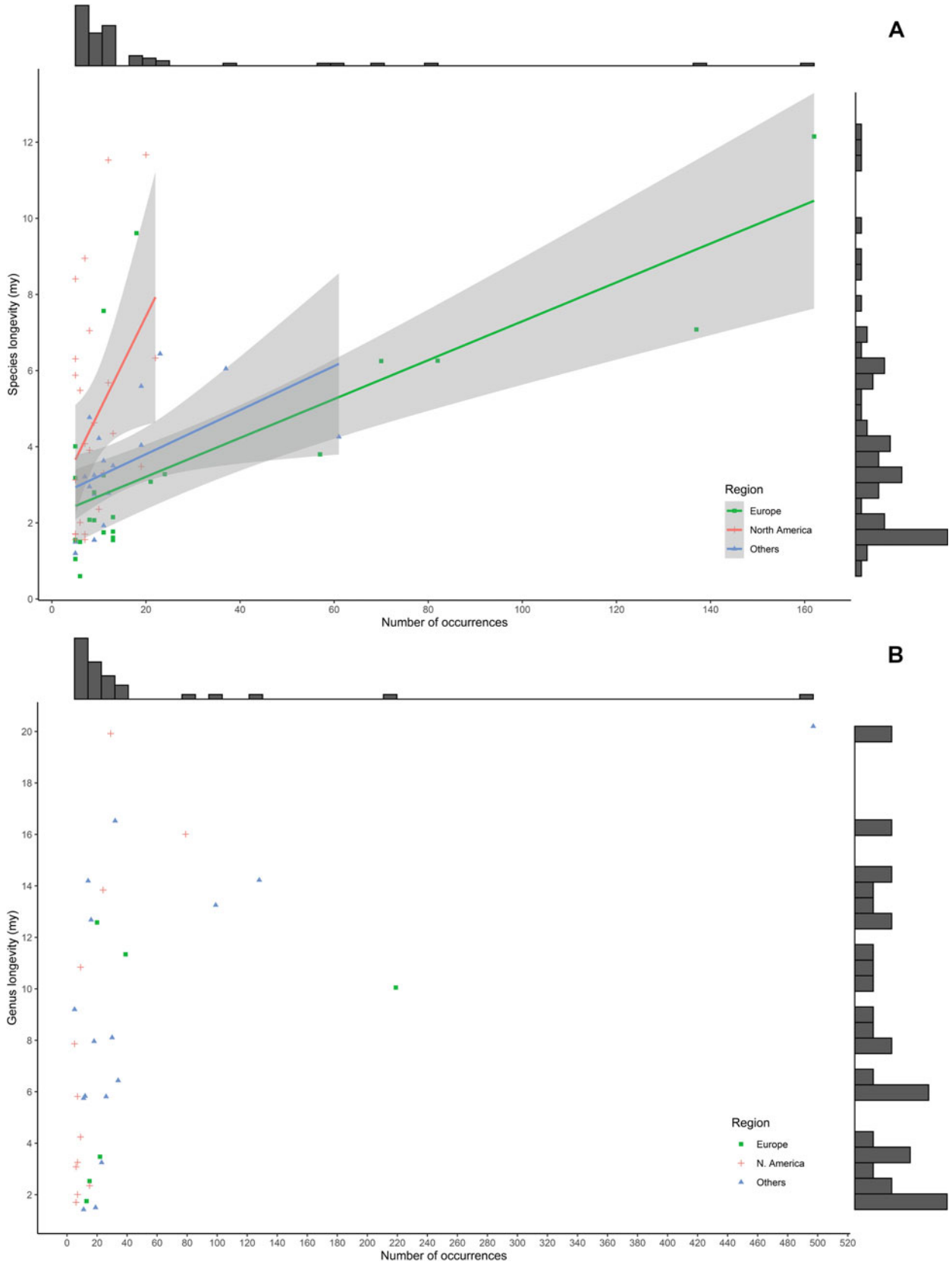

Fig. 8.2 Relation between the number of occurrences and the longevity of eulipotyphlans, with marginal representation of distribution, for species longevity (**A**) and genus longevity (**B**). European species are represented by green squares, North-American species by red crosses, and species from other zones by blue triangles. Species and genera with a range of 0 are not considered. Equations are provided in Appendix 8.1

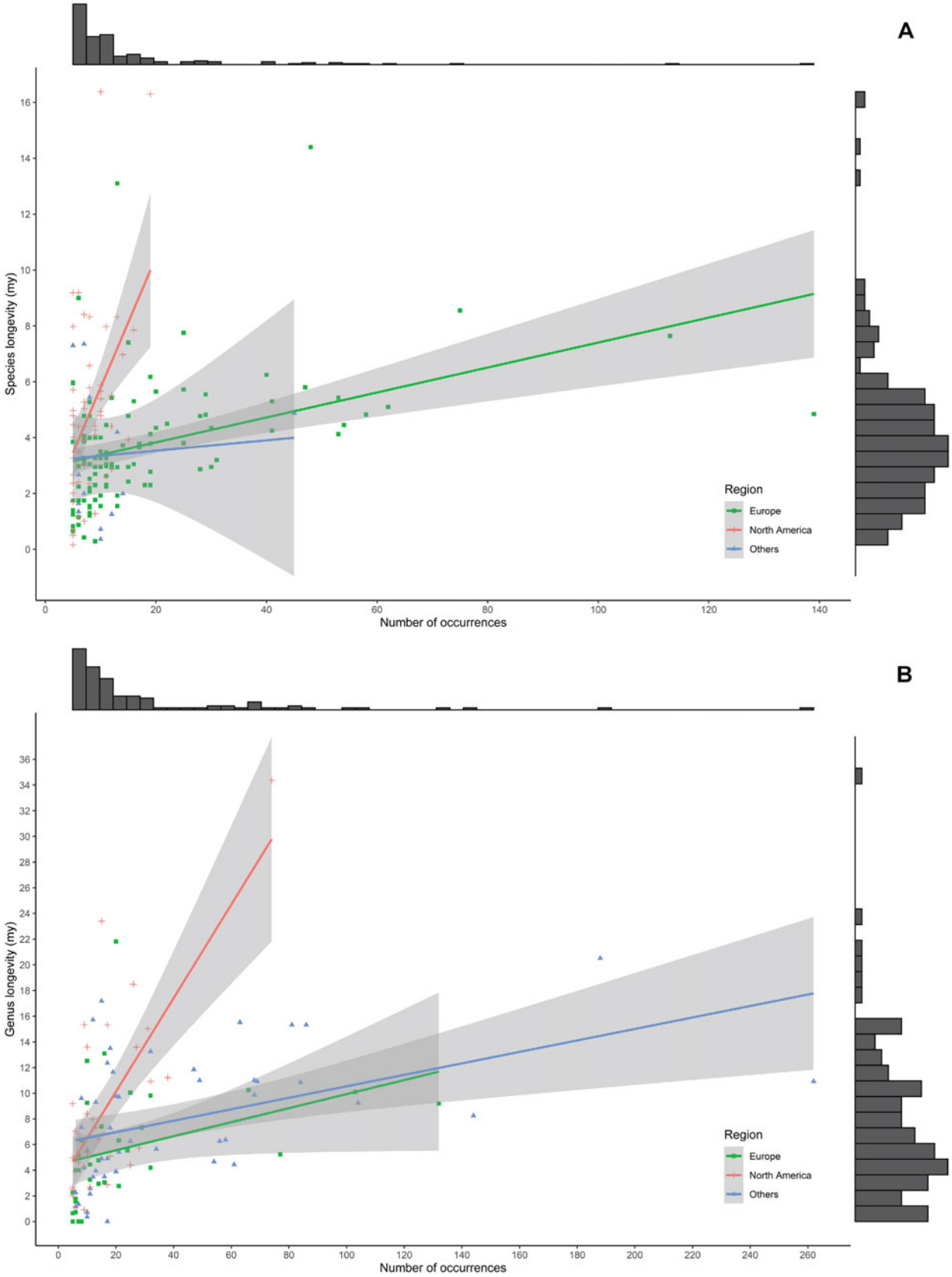

Fig. 8.3 Relation between the number of occurrences and the longevity of lagomorphs, with marginal representation of distribution, for species longevity (**A**) and genus longevity (**B**). European species are represented by green squares, North-American species by red crosses, and species from other zones by blue triangles. Species and genera with a range of 0 are not considered. Equations are provided in Appendix 8.1

subfamily. At the other end of the spectrum, we find the mostly Paleogene Eucricetodontinae, with a median of 7.80 my. As we noted with the families, a number of low-diversity subfamilies for which no boxplot was constructed have an even longer median genus longevity. These are the Anomalomyinae (9.01 my), Eumyarioninae (9.25 my) and Dendromurinae (10.45 my).

When we consider the boxplots for rodents at the species level, again we see differences between the various families, but much less pronounced than for genera. The Mylagaulidae stand out with a median duration of 6.84 my. The median species durations found for the other families lie between 1.50 my (Geomyidae) and 5.23 my (Castoridae). Again, the Muridae with 1.90 my is among the families with the shortest durations. The two families with shorter durations (Geomyidae and Hystricidae) have, respectively, only eight and ten species for which longevity has been calculated (i.e., species with more than five occurrences in the database). From these, both families have two species which occur in one time unit only, which in our analyses give a duration of zero, and three hystricids and one geomyid are extant species. As such, the short durations of these families could well be an artefact. Certainly, the notable difference we found between the median and average species duration of Geomyidae (1.50 my vs. 4.19 my) calls for caution when considering these data. In all other families, these two values generally differ no more than 1 my, with the exception of the Heteromyidae, Sciuridae and Castoridae. The common denominator for these families and Geomyidae is that they all have genera with an exceptionally long duration, as we will discuss in more detail for the sciurids and castorids below.

Discussion

Taxonomy and Longevity

Ultimately, any database study is dependent on the quality of individual data points, whether dealing with misidentifications or with basic taxonomical issues. Prothero (2014), for instance, commented on the quality of the North American record, leading him to exclude some records from his analysis. Taxonomic debates often revolve around the issues of splitting or lumping taxonomic units and can involve both the species and the genus level. A clear case where oversplitting can be suspected is the record of the Geomyidae. We already noted that this was the family with the shortest median species longevity (1.50 my), but that was probably an artefact of the low number of species (n = 8) for which a duration had been calculated. Looking at the family as a whole, our dataset comprised 126 species occurrences of Geomyidae and no less than fifty different species. Such a record suggests that the current classification of the fossil representatives of Geomyidae is probably oversplit. A review synonymizing nominal species would lead to combining more records per species and increase the median and average duration. Of course, given that in particular the genus classification is strongly influenced by individual preferences, more such issues will exist, even in a database which strives for maximal consistency such as the NOW (Žliobaitė et al. 2023).

Excessively long longevities for a species could also indicate a taxonomical problem. This is well illustrated by Holroyd and Stevens (2009), who considered the over 13 my range of *Phiomys andrewsi* suspicious. Moreover, the record comprises finds from the Early Oligocene of Egypt and the Early Miocene of Kenya, thus showing a temporal and geographical separation. Taxonomic revision showed that the Miocene record belonged to a separate genus and species, *Lavocatomys aequatorialis*. Long taxon durations served as a red flag in our analyses, as, for instance, was the case for Miocene Iberian glirid *Armantomys*, which yielded an overly long longevity because of an erroneous record in the Pliocene of Poland.

Liow et al. (2008) argued that small mammals were less prone to extinction because of the Sleep or Hide strategy (SLOH), by which animals reduce metabolic and predatory pressure by, for instance, hibernating and building burrows. In fact, the median genus duration of small and large mammals (2.4 my and 2.2 my) in their study differs little and the histograms of duration followed mostly a similar pattern. The major difference lies in the genera with a very long (>14 my) duration, which in their analysis comprised only one large mammal versus 17 small mammal genera. The genera in question are listed in their supplementary material. In our analyses, eight out of the seventeen have a very long duration, the others apparently having been resolved in subsequent updates of the database. On the other hand, partly because of the wider scope of our study, we found another 37 genera with a duration of over 14 my. The vast majority of these are from North America and will, given the earlier mentioned problems with that record, not be included in the discussion. However, given the large number of long-lived small mammal genera in Europe, we would expect that some North American genera also have in fact a similarly long duration. In Table 8.4, we list the European genera with a range of over 14 my.

It is clear from Table 8.4 that indeed a large number of small mammal genera have long durations. The Sciuridae and Gliridae stand out, with six and five genera with a duration over 14 million years, respectively. The presence of the long-lived glirid genera could be seen as support of the SLOH hypothesis as a strategy guarding against extinction. After all, Gliridae are known for their capacity to hibernate. Three out of the six squirrels are ground squirrels, which

Table 8.4 Small mammal genera with durations longer than 14 my

Taxa	Genus	Longevity (my)	Taxa	Genus	Longevity (my)
Rodentia			Castoridae	*Steneofiber*	14.1
Sciuridae	*Blackia*	20.1	Dipodidae	*Plesiosminthus*	16.8
Sciuridae	*Miopetaurista*	15.3	Dipodidae	*Heterosminthus*	19.2
Sciuridae	*Hylopetes*	16.8	Muridae	*Eucricetodon*	14.9
Sciuridae	*Spermophilinus*	16.3	Ischyromyidae	*Paramys*	14.2
Sciuridae	*Heteroxerus*	16.9	Ischyromyidae	*Microparamys*	16.9
Sciuridae	*Atlantoxerus*	18.4	**Lagomorpha**		
Gliridae	*Glirulus*	17.4	Ochotonidae	*Prolagus*	20.2
Gliridae	*Microdyromys*	25.1	**Eulipotyphla**		
Gliridae	*Glis*	22.3	Talpidae	*Desmanella*	15.6
Gliridae	*Muscardinus*	16.2	Talpidae	*Talpa*	20.5
Gliridae	*Vasseuromys*	14.9	Talpidae	*Myxomygale*	21.8
Castoridae	*Euroxenomys*	15.3	Soricidae	*Paenelimnoecus*	15.3

would fit the 'hide' component of SLOH. However, the other three long-lived genera are flying squirrels, which do not fit the bill. Moreover, the largest rodent family, the murids, occupies a wide variety of niches including many burrowing forms, yet only one genus, *Eucricetodon*, has a duration of over 14 million years. Turning to the insectivores, we note one typical burrower, *Talpa*, on the list, but also *Desmanella*, a uropsiline talpid with next to no burrowing capacity, features on the list. So the Sleep or Hide Strategy does not seem a consistent common denominator to explain the extended duration of these small mammal genera.

Part of the explanation why in particular dormice and squirrels have these long-lived genera may be quite mundane. The most widely followed classification for fossil glirids is based on dental morphology alone (Daams & De Bruijn, 1995). The choice for using only dental characteristics was made because 'this is the only character known for all taxa'. However, the authors themselves indicated that this type of classification has limitations. The genera *Glamys* and *Gliravus* have different types of skulls (Vianey-Liaud, 1989), but were synonymized because of the similarity of their dentitions. In addition, the genera *Dryomys*, *Graphiurus* and *Leithia*, despite also having different skull types, all ended up classified in the same subfamily. A classification based solely on dental morphology is limited for characters to distinguish taxonomic groups. Fossil Gliridae are mainly described on the basis of the number of ridges and the connections between them and the concavity of the occlusal surface. There are only so many permutations of the dental morphology available. Moreover, these permutations also are ecologically constrained. Van der Meulen and De Bruijn (1982) demonstrated that within the Gliridae ecomorphotypes can be recognized, with forms from a forested environment displaying more dental ridges than those from open landscapes.

A similar explanation could apply to the Sciuridae. The dental pattern of squirrels is quite conservative and also allows for a limited number of morphologies. Bouwens and De Bruijn (1986) showed that the recent genera *Hylopetes* and *Petinomys* could not be distinguished on the basis of their dentition. Only quite recently, tentative finds of the recent Asian genus *Ratufa* from the Miocene of Europe were described as a separate genus, *Dehmisciurus* (Markovic et al., 2016). Similarly, the European finds of *Hylopetes* were transferred to *Neopetes* by Daxner-Höck (2004). That classification is not followed in the NOW database, but should it be incorporated, it would greatly shorten the duration of *Hylopetes*. Given these examples, the question is justified whether, for instance, the European Miocene finds of *Atlantoxerus* actually belong to the same clade as the recent African forms of that genus (Pablo Pelaez-Campomanes, pers. comm.).

To a certain extent, the high number of glirids and sciurids on our list of long-lived genera also reflects that the two are the second-most and third-most diverse families in our dataset and therefore have a larger chance to also have long-lived genera. In that respect it is noteworthy that the Castoridae, with a far lower number of genera, features two long-lived taxa. However, it must be noted that the taxonomic problems in the group are notorious (Casanovas-Vilar & Alba, 2011). As we already mentioned, the most diverse rodent family, the Muridae, only has one representative on the list. In contrast to the Gliridae and Sciuridae, the molar morphology is highly variable. Some subfamilies deviate so strongly from the basal murid pattern that they require a dental nomenclature of their own. It is, therefore, by no means a coincidence that in particular paleontologists favor raising some murid subfamilies to the family level. Still, even within the more basic pattern, the family shows a lot of diversity in the morphology of the main cusps and the ridges between them. It is the large variety of forms, each with their

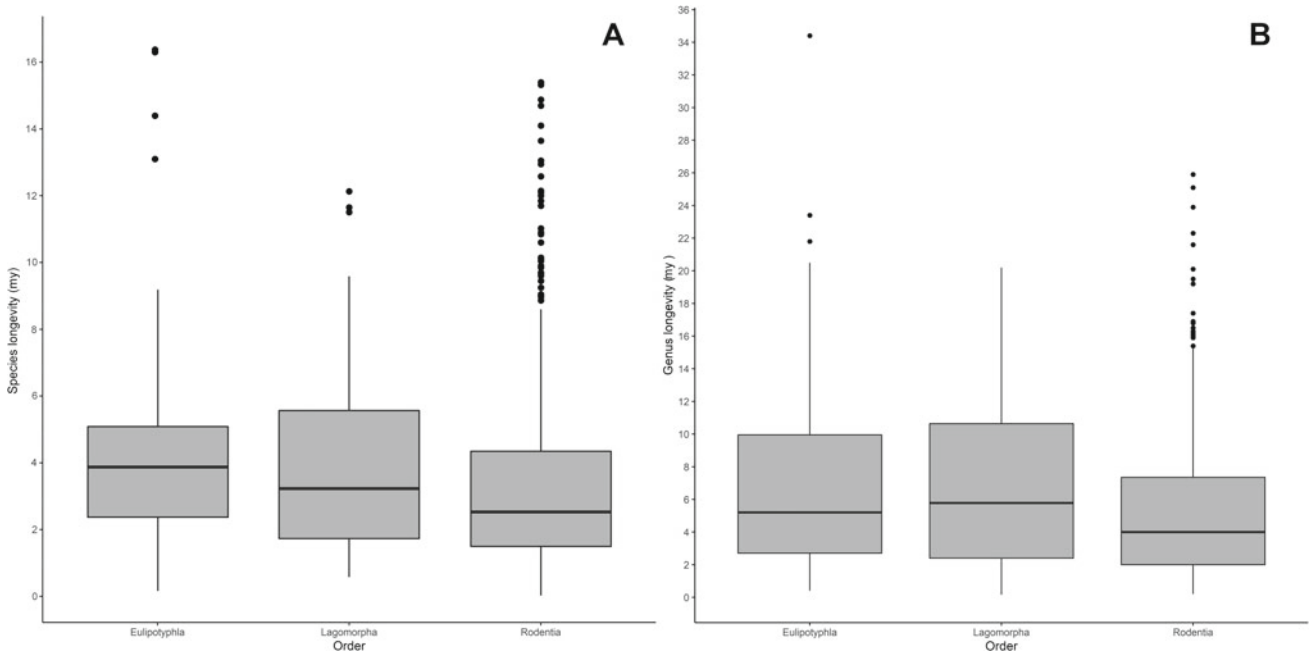

Fig. 8.4 Distribution of species longevity and genus longevity among Eulipotyphla, Lagomorpha and Rodentia. Species with a range of 0 are not considered

own temporal range, that makes murids such an important group for stratigraphic purposes. In return, the group may have had more attention from scholars in an attempt to define (chrono)-species that can be used in their stratigraphic schemes. Certainly, it is the group in which most lineages have been proposed. Van der Meulen et al. (2003), for instance, recognized various subsequent chronospecies in two lineages of middle-sized *Democricetodon* in the Daroca basin (the *D. hispanicus-D. moralesi-D. jordensi-D. lacombai* and *D. franconicus-D. koenigswaldi-D. larteti-D. crusafonti* lineages). Of course, the transitions from one chronospecies to another do not mark true extinctions. Flynn et al. (1995) aptly called these transitions 'pseudo-extinctions' and it is notable that the combined duration of these lineages in the basin roughly equals some of the ranges of glirids and sciurids from the same area that are classified as a single species. Thus, in this case, using a strictly phylogenetic species concept implies that the differences in longevity would be far less. However, we concur with Flynn et al. (1995) that, in terms of stability of the ecosystem, pseudo-extinctions provide meaningful information. Moreover, in biological terms it is interesting to understand why the murids showed rapid bursts of evolution (involving mainly size increase in the given example), whereas other groups do not. The most important reason for using chronospecies rather than lineages in our analyses, however, is that well-defined lineages, such as those described by Van der Meulen et al. (2003), are an exception. For most species we simply do not know the ancestors or the descendants.

Diversity and Longevity

Smits (2015) found a significant phylogenetic effect in the longevity of mammals in the North American Cenozoic record. This is in line with our findings that there are significant differences between various taxonomic groups. Of course, phylogeny in itself does not explain the differences in longevity. To find a possible causality, we need to focus on which groups show a relatively short or long longevity and what these groups have in common.

One pattern that emerged in our analyses is that taxonomic groups with a higher diversity tend to display shorter median longevities. This is apparent at all taxonomic levels. The rodents demonstrate considerably shorter median longevities than either the insectivores or the lagomorphs (Figs. 8.4, 8.5, 8.6, 8.7 and 8.8), whereas within the rodents and insectivores the most diverse family, respectively the Muridae and Soricidae, have the shortest longevities. We noticed earlier that the high number of possible permutations in the murid molar and recognition of chronospecies may have somewhat inflated diversity in the murids. By contrast, the molar morphology in Soricidae is notably conservative, yet the family still shows the shortest median duration for genera among the eulipotyphlans. In addition to the short ranges for taxa in the more diverse families, the longest longevities are found in the least diverse families, such as the Distylomyidae for rodents or the Plesiosoricidae in the case of the eulipotyphlans.

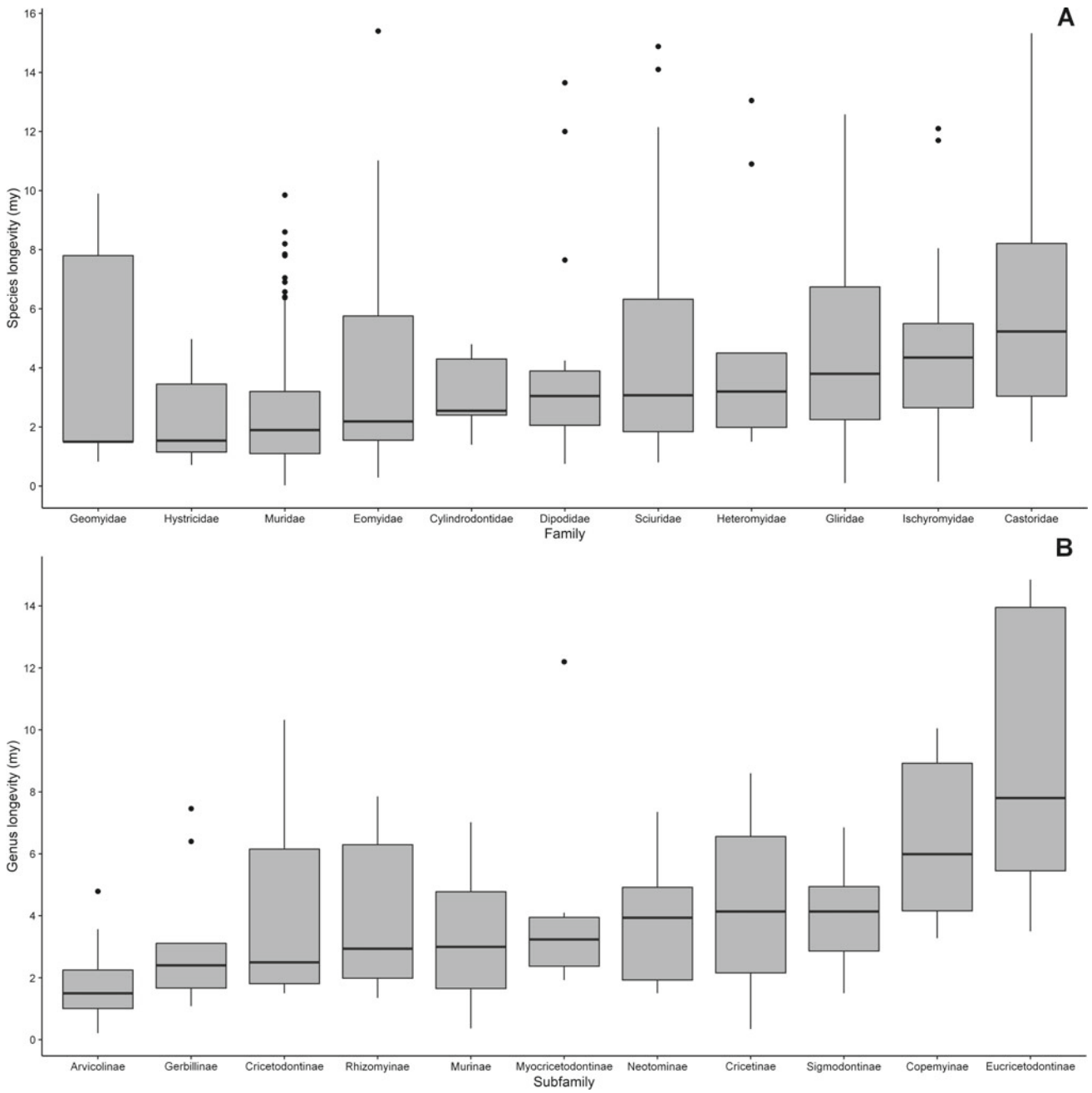

Fig. 8.5 Distribution of species longevity in rodent families (**A**) and genus longevity in Muridae subfamilies (**B**). Families and subfamilies with less than five species are excluded. Species with a range of 0 are not considered

Given that modern rodent families first appeared around the Eocene/Oligocene boundary, it seems logical that the most diverse family shows the shortest longevities. After all, in order to obtain a larger diversification in the same period of time, there must have been an increased rate in branching. One has to be careful with this line of reasoning, though, as we are also dealing with families that are extinct (e.g., Eomyidae, Dimylidae) and some families had their largest diversity in the past. The Gliridae, for instance, had the largest diversity in the Middle Miocene (e.g., Lu et al., 2021) and the Early Miocene was the heyday for the Talpidae. Moreover, theoretically, an early diversification could also result in long-lived genera in the more diverse families. This, however, does not appear to be the case. Instead, the Muridae 're-invented' themselves with subsequent radiations of cricetine type taxa in the Oligocene and Middle Miocene, followed by radiations of the Murinae and Arvicolinae at the beginning of the Late Miocene and Early Pliocene,

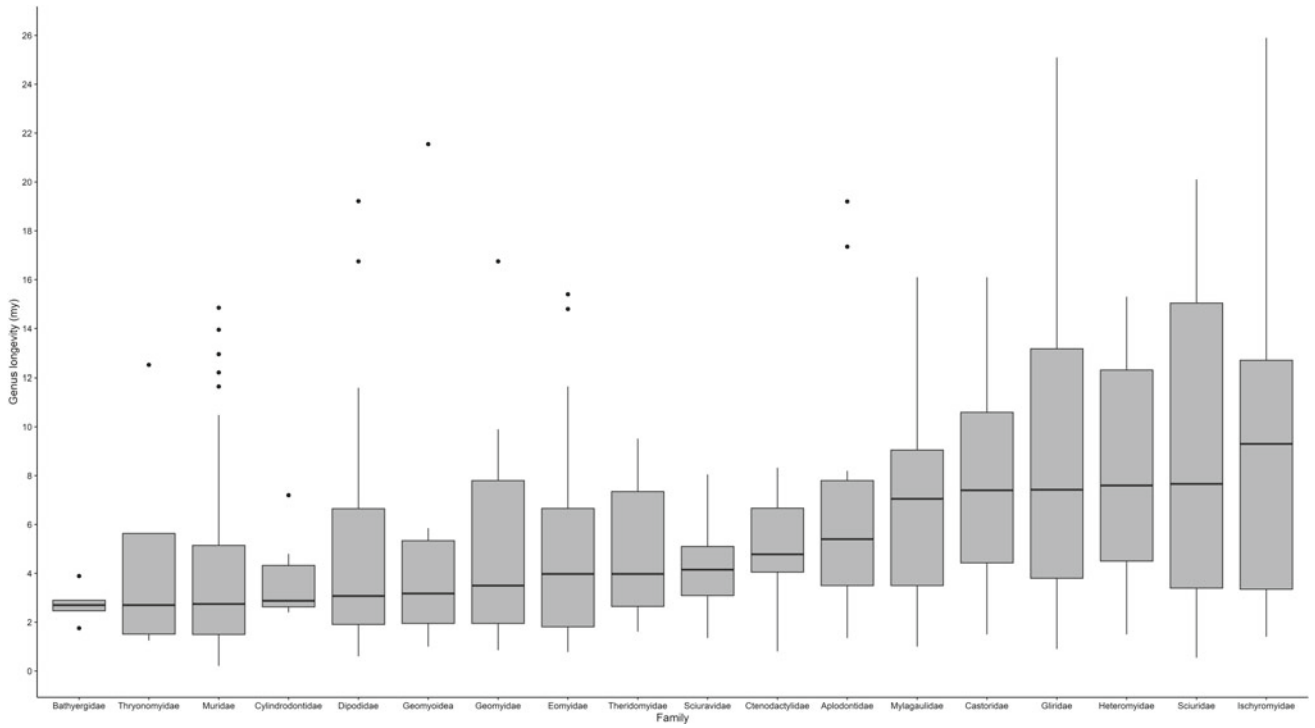

Fig. 8.6 Distribution of genus longevity in rodents families. Families with less than five genera are excluded. Species with a range of 0 are not considered

respectively. According to Van den Hoek Ostende et al. (2020), the last radiations in particular lead to an increase in rodent diversity in Europe. By contrast, the diversification of the Soricidae only started in the Middle Miocene, following a period in which the Talpidae were the most diverse eulipotyphlan family.

Whereas a high diversity implies higher evolutionary rates to account for the higher number of branches, it will also promote evolution through increased competition. Apart from being diverse, Muridae are also abundant in fossil assemblages for most of the Neogene and are usually represented by multiple genera and species. Galbrun et al. (2023) discussed the patterns in localities with congeneric species and kindly made their matrix for small mammals available to us. From their data it is apparent that in particular murids frequently appear in localities with multiple species of the same genus. The highest ranking among these are *Mimomys* (115 localities), *Democricetodon* (66 localities), *Megacricetodon* (52 localities), *Microtus* (48 localities) and *Apodemus* (21 localities). The highest score in Europe for a non-murid is that of *Microdyromys* (19 localities). Quite peculiar is that the highest scoring rodent in the American record is the geomyid *Entoptychus* (29 localities). As for the eulipotyphlans, the genus with the highest number of co-occurring species is *Sorex* (46 localities).

Darwin (1859) postulated that phylogenetically closer related species would be in stronger competition with one another, because of the similarity in structure and also in habitat. In small mammal paleontology, this would certainly be expected to be the case, as the similarity in structure (i.e., in the dentition) is directly related to a similarity in adaptations for food processing. Cahill et al. (2008) found little support for stronger competition between more related species in their study of vascular plants. Taking a community point of view and investigating whether a pattern of exclusion between congenerics could be found in the NOW database, Galbrun et al. (2023) only found a weak pattern. Of course, closely related species can co-occur if they adapt to a pattern of niche partitioning, and we can assume that some type of partitioning exists whenever we find congenerics within a single fossil assemblage. This does not necessarily imply that the interspecific competition leads to exclusion or even extinction of one of the two taxa. It does lead to a more dynamic system in which closely related species are prone to co-evolution. Earlier, we mentioned the example of the *Democriceton*-lineages in the Middle Miocene of northeastern Spain described by Van der Meulen et al. (2003). These lineages show strictly parallel changes and simultaneous transitions between their chronospecies (which we marked as pseudoextinctions). These parallel changes suggest that there is some form of interaction in the evolution of the congenerics which may account for the *Democricetodon* species evolving whereas other small mammal species in the section remain relatively unaltered.

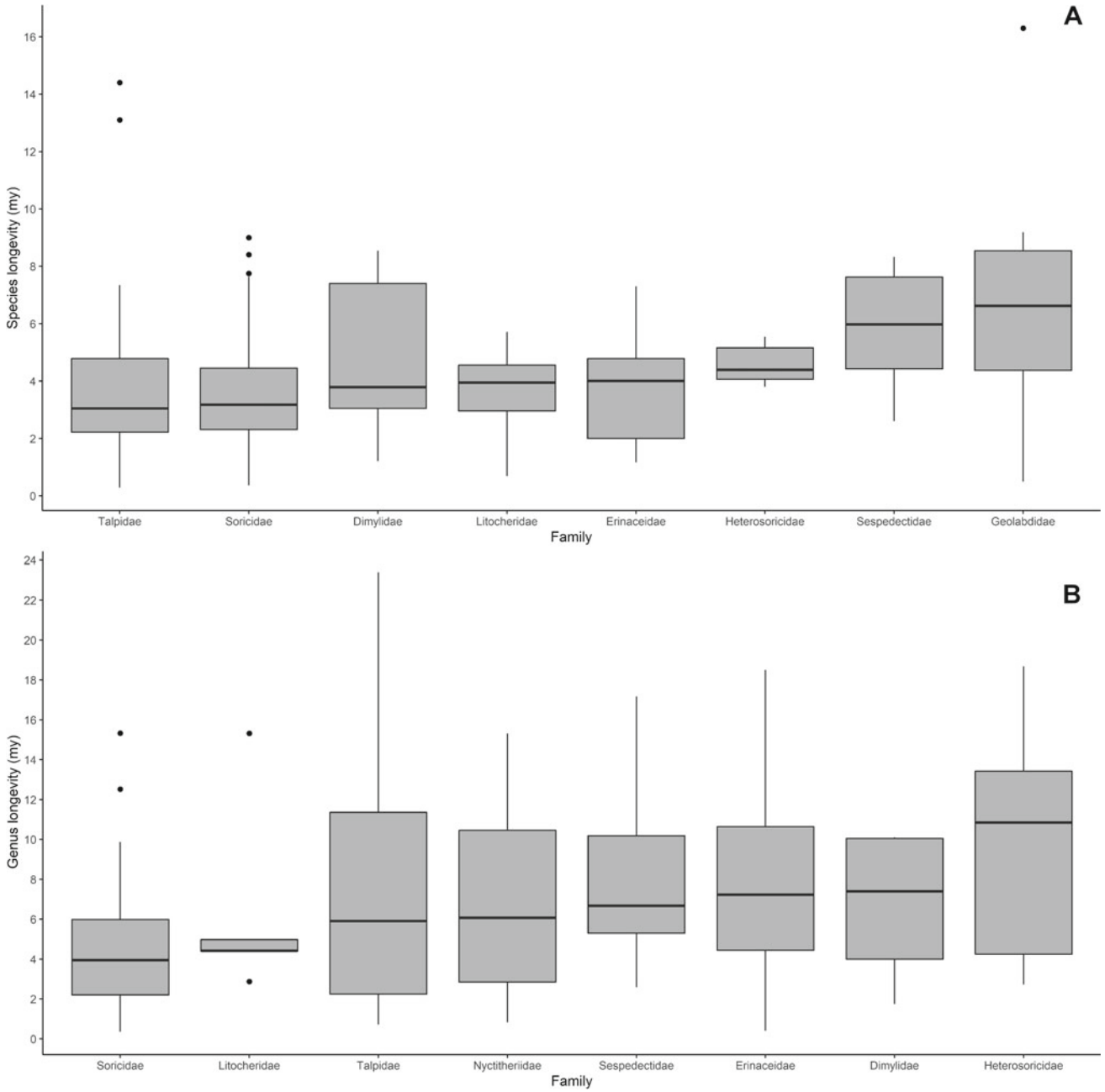

Fig. 8.7 Distribution of species longevity (**A**) and genus longevity (**B**) in eulipotyphlan families. Families with less than five genera are excluded. Species with a range of 0 are not considered

An example on how diversity and evolutionary rates are related is the history of the murid genus *Eumyarion*. This hamster dominates the Early Miocene small mammal assemblages of Anatolia, with up to three species occurring in the same locality (De Bruijn & Saraç, 1991; De Bruijn et al., 2006; Bilgin et al., 2019; Joniak et al., 2017, 2019; Pelaez-Campomanes et al., 2019). During this period, the genus undergoes rapid evolution, to the point that almost each locality has its own species of middle-sized *Eumyarion*. As a result, we could not calculate any longevities for the Anatolian *Eumyarion* species, having set the limit at species with five occurrences or more. This is in contrast to the Middle Miocene European record, where *Eumyarion* is far less abundant. Here, species longevities range up to 6.6 my, well above the median length of the Muridae.

In the given examples of *Democricetodon* and *Eumyarion* species, it is easy to envision how evolution is directly influenced by interspecific competition. Here, Red Queen dynamics result in relatively fast changes allowing congeneric species to continue their co-occurrence as long as

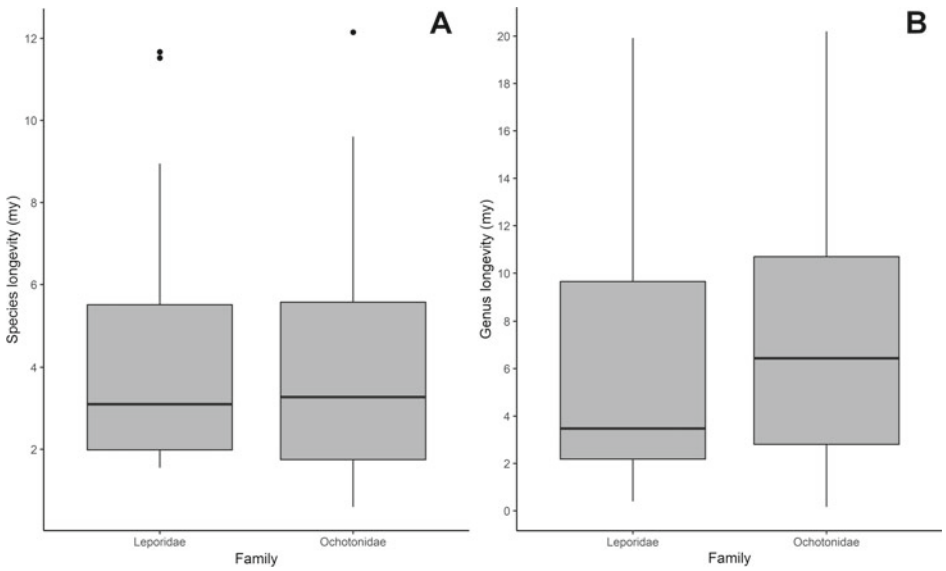

Fig. 8.8 Distribution of species longevity (**A**) and genus longevity (**B**) in lagomorph families. Species with a range of 0 are not considered

ecosystems can sustain their combined presence. While the dynamics are quite obvious at the species level, accounting for shorter species longevities, they are perhaps less clear at the genus level. The shorter longevities for genera in the more diverse families can be attributed to the same dynamics even though competitive pressures will be less direct. After all, the more similar two taxa are in structure, the more likely they are to have some degree of competition. Deviating structures, on the other hand, will allow for better niche partitioning. Also in this respect, the history of *Eumyarion* is interesting. It is one of the longest living murid genera (13.5 my) and, as we noted, the younger species also rate among the longer-lived murids. Notably, the morphology of the molars is far more complicated than that of other Middle Miocene murids, such as *Democricetodon* and *Megacricetodon*. Thus, the history of the genus is subdivided into two parts. During the time when its morphology was predominant in the Early Miocene of Anatolia, *Eumyarion* showed high evolutionary dynamics, after which the same morphological characteristics allowed it to secure its own stable niche in the Middle Miocene of Europe, resulting in overall a long duration of the genus.

The pattern found for *Eumyarion* is mirrored in that of other long-lived genera. The longest duration for a murid is found in *Eucricetodon* (14.9 my). This genus is part of the Oligocene radiation of hamsters, but stands out as being one of the few genera that survives into the Early Miocene, even up to the so-called "Cricetid Vacuum" in MN 3 (Freudenthal & Martín-Suárez, 2016; Sesé, 1987). *Glis* and *Glirulus* are two extant glirid genera with durations of 22.3 and 17.4 my, respectively. Thus, both were also part of the Middle Miocene high in glirid diversity, but, unlike other genera, continued in the late Neogene and Quaternary. These examples are not just to state the obvious, namely that survivors live longer. The point we are trying to make is that, once a period of high diversity has ended, the surviving taxa will have less competition from similar forms and are able to continue relatively unaltered for an extended period of time. It pays off to stand apart. In this respect, it is perhaps not a coincidence that *Glis* and *Glirulus*, in terms of the number of dental ridges, are at the ends of the spectrum, with respectively a minimal and maximal number. In addition, the third long-lived Neogene glirid, *Muscardinus* (16.2 my), has an atypical morphology with its extended first molars. This genus originated at the end of the period of maximum glirid diversity, showing that not only genera 'surviving' a period of maximal diversity can be long-lived, but also that newcomers can benefit from having little competition. This is emphasized by the situation in the Eomyidae. The two longest-living European genera, *Keramidomys* (11.7 my) and *Eomyops* (11.0 my) both appeared after the Early Miocene, the heyday of the family on the continent.

If indeed having a niche of your own with little competition is one of the key factors in promoting longevity, it makes sense that beavers have a longer median longevity and that *Euroxenomys* and *Steneofiber* are among the longest living genera. However, as we noted before, there are many issues in beaver taxonomy that need to be resolved to ensure this pattern. In Sciuridae, longevity may also be in part related to taxonomy and the inability to distinguish between genera based on dentition alone (e.g., Bouwens & De Bruijn, 1986). This is presumably the case for *Hylopetes* (16.8 my), which, if we transfer some of its species to *Neopetes* as suggested by Daxner-Höck (2004) would no longer be

long-lived. The remaining long-lived genera, *Miopetaurista* (15.3 my), *Blackia* (20.1 my), *Spermophilinus* (16.3 my), *Heteroxerus* and *Atlantoxerus* largely show an overlap in their ranges. *Miopetaurista* and *Blackia* are flying squirrels, which fall at two ends of the size spectrum, the first falling in the range of the present-day giant flying squirrels (Casanovas-Vilar et al., 2018), the other among the smallest in the group. So it is clear that there would have been little competition between them. Such an explanation is, however, not as readily apparent for the two ground squirrels *Spermophilinus* and *Heteroxerus*.

Among the eulipotyphlans we find three talpids and a soricid as the longest living genera, which is at first sight remarkable, as these are representatives of the two most diverse eulipotyplan families. *Desmanella* (15.3 my), however, is the only uropsiline talpid in Europe during most of its range. While it is thus the mole least adapted to a burrowing lifestyle, the longest duration for an eulipotyphlan is found in *Talpa* (20.5), which is by contrast the genus most adapted to burrowing. *Paenelimnoecus* (15.3 my) is a shrew which, because of its unique characteristics, is not easily qualified, to the point that Fejfar et al. (2006) suggested to erect a separate subfamily just for this genus. So among the eulipotyphlans as well we see that the longest living genera are those that either hold a position of their own or are at the ends of the morphological spectrum. In either case, these taxa hold a position with limited competition from their relatives.

The overall pattern that emerges is one of a fast and a slow lane of evolution. In the fast lane, diversification is high and the continuous interspecific competition leads to a rapid succession of (chrono)-species. The species in the slow lane hold a relatively unique position and are often at the edge of the morphological or metrical variation of their group. Thus, limited competition allows them to persist longer. In this respect, there is some analogy with the fast-slow continuum in mammals (e.g., Dobson & Oli, 2007; Oli, 2004). Here, the fast lane shows a higher intraspecific competition than the slow lane, due to higher reproduction, and is characterized by short (individual) longevities whereas the longest longevities are found at the slow end of the spectrum.

If higher diversity leads to shorter durations of taxa, we can surmise that at the beginning of diversification we would have more long-lived taxa. This would account for the temporal component that Smits (2015) found in assessing longevities. However, these findings were opposite those of Flynn et al. (1995), who found shorter durations in the Paleogene of Wyoming than in their Neogene sequence. At present, we consider the quality of the Paleogene record in the NOW insufficient to reliably conclude on the prerequisite of this question, namely if Paleogene diversity is indeed lower than that of the Neogene. However, this does present a tantalizing question for future research.

Conclusions

The median longevities found in this study for rodents, eulipotyphlans and lagomorph species (respectively 2.53, 3.85 and 3.15 my) are in the same order of magnitude as the mammal longevities in previous studies. There is a considerable variation in the species and genus duration within and among different taxonomic groups. This is the first study that examines longevities within the small mammals and, as is known from large mammals, we found phylogeny (as indicated by taxonomy) is an important factor in different durations.

Small mammal taxonomy is almost exclusively based on dental morphology. This can influence analyses, as the number of permutations within a molar type can be limited. As such, the question is justified whether the Miocene representatives of genera as *Atlantoxerus* or *Glirulus* are truly ancestral to the recent species. Monophyly may be questioned for some of the small mammal genera with an excessively long duration (>14 my). Some groups, such as the beavers, have taxonomies that are still very much under debate. Our analyses even suggest that the North American record as a whole suffers from a number of taxonomic issues, leading to short longevities in case of splitting and long longevities in the case of lumping taxonomic data.

Overall, a pattern emerges in which the groups with the largest diversity (murids, soricids) show the shortest median longevity. On the other hand, longer taxa durations are common in groups with low diversity. Looking in detail at the genera with a duration of over 14 million years, we see that these are generally taxa that form a minor part of assemblages, at least for a major part of their range. Where we find long-lived genera from the same family with similar ranges, these are often taxa at the edge of the spectrum in morphology (*Glis, Glirulus*), size (*Miopetaurista*, *Blackia*) or life style (*Talpa*, *Desmanella*). This pattern suggests that lack of competition is a driving factor in longevity. Interspecific competition in diverse and abundant groups lead to a high Red Queen dynamics, which results in a rapid sequence of (chrono)-species. Taxa that on the other hand have a niche of their own with little competition are capable of remaining relatively unaltered for a long period of time, provided that their niche remains available.

Appendix 8.1

Equations of the linear regression models applied on species and genus longevity, represented in Figs. 8.1, 8.2 and 8.3

Taxa	Species-level				Genus-level			
	region	n	y	R^2	region	n	y	R^2
Rodentia								
	Europe	357	0.054x + 1.980	0.311	Europe	80	0.041x + 4.329	0.249
	North America	116	0.209x + 2.681	0.068	North America	122	0.164x + 4.668	0.132
	Others	136	0.559x + 2.205	0.080	Others	175	0.021x + 4.696	0.154
	Total	609	0.049x + 2.470	0.164	Total	377	0.023x + 5.371	0.102
Lagomorpha								
	Europe	25	0.051x + 2.186	0.540	Europe	6	/	/
	North America	27	0.251x + 2.40	0.170	North America	12	/	/
	Others	19	/	/	Others	16	/	/
	Total	71	0.044x + 3.199	0.207	Total	34	0.030x + 6.848	0.250
Eulipotyphla								
	Europe	112	0.045x + 2.936	0.171	Europe	30	0.045x + 5.205	0.089
	North America	54	0.467x + 1.127	0.223	North America	32	0.364x + 2.852	0.509
	Others	15	/	/	Others	47	0.043x + 6.279	0.199
	Total	181	0.038x + 3.507	0.061	Total	109	0.055x + 5.904	0.138

Appendix 8.2

Species of long duration detected through the IQR criterion. Species from families with less than five species and/or a range of 0 are excluded. Nb.Occ = number of occurrences

Taxa	Family	Longevity (my)	Nb. Occ	Region
Rodentia				
Democricetodon gaillardi	Muridae	6.90	20	Europe
Myocricetodon parvus	Muridae	6.91	8	Africa and Europe
Copemys esmeraldensis	Muridae	7.05	6	North America
Paciculus insolitus	Muridae	7.80	5	North America
Leidymys nematodon	Muridae	7.80	6	North America
Democricetodon kohatensis	Muridae	7.85	11	Asia
Copemys dentalis	Muridae	8.20	10	North America
Copemys russelli	Muridae	8.60	6	North America
Anomalomys gaudryi	Muridae	9.85	51	Europe
Adjidaumo minimus	Eomyidae	15.40	25	North America
	Sciuridae	14.10	74	Europe
Heteroxerus grivensis				
Blackia miocaenica	Sciuridae	14.88	64	Europe
Protalactaga tunggurensis	Dipodidae	7.65	6	Asia
Heterosminthus orientalis	Dipodidae	12.00	18	Europe and Asia
Plesiosminthus clivosus	Dipodidae	13.65	9	North America
Perognathus furlongi	Heteromyidae	10.90	14	North America
Perognathus minutus	Heteromyidae	13.05	9	North America
Thisbemys perditus	Ischyromyidae	11.70	9	North America
Microparamys minutus	Ischyromyidae	12.10	13	North America
Lagomorpha				
Hypolagus gidleyi	Leporidae	11.53	12	North America
Hypolagus vetus	Leporidae	11.67	20	North America
Prolagus oeningensis	Ochotonidae	12.15	162	Europe
Eulipotyphla				

(continued)

Taxa	Family	Longevity (my)	Nb. Occ	Region
Yanshuella primaeva	Talpidae	7.35	7	Asia
Urotrichus dolichochir	Talpidae	13.10	13	Europe
Talpa minuta	Talpidae	14.40	48	Europe
Petenya dubia	Soricidae	7.75	25	Europe
Limnoecus tricuspis	Soricidae	8.41	7	North America
Deinsdorfia kordosi	Soricidae	9.00	6	Europe
Centetodon magnus	Geolabdidae	16.60	10	North America

Appendix 8.3

Geographic distribution of Rodentia, Lagomorpha and Eulipotyphla genera whose duration has been calculated, including the number of species extracted from these genera

Taxa	Rodentia		Lagomorpha		Eulipotyphla	
Level	Species	Genus	Species	Genus	Species	Genus
Europe	456	153	28	14	137	65
Asia	260	131	15	9	45	45
Africa	165	99	8	4	3	2
North America	**685**	**238**	57	**24**	**153**	**74**
South America	126	87	0	0	0	0
Europe and Asia	508	60	28	7	146	31
Africa and Asia	56	11	0	0	8	1
Africa and Europe	40	6	23	1	5	1
North America and Asia	12	4	7	1	5	2
North America and South America	2	1	0	0	0	0
Africa, Europe and Asia	154	13	9	1	41	4
Asia, Europe and North America	154	17	**60**	3	68	6
Europe and North America	41	4	2	1	22	5
Australia	2	2	0	0	0	0
Europe, Asia, Africa, North America	0	0	0	0	15	1
Total	2261	826	237	65	648	237

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