Supporting Information

Evolution of degrees of carnivory and dietary specialization across Mammalia and their effects on speciation

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21 **Supplementary Tables**

Table S1. The number of regime shifts in degree of carnivory and dietary specialization across Mammalia

Clade	Degree of carnivory		Degree of dietary specialization	
	Number of shifts (proportion of species number)	Standard deviation of optimum value in extant species	Number of shifts (proportion of species number)	Standard deviation of optimum value in extant species
Artiodactyla + Perissodactyla	26 (0.087)	40.2	21 (0.070)	17.3
Atlantogenata	5 (0.072)	34.2	5 (0.072)	12.5
Carnivora + Pholidota	17 (0.067)	18.6	8 (0.032)	16.0
Castorimorpha	6 (0.066)	6.2	9 (0.099)	29.4
Chiroptera	54 (0.074)	37.5	60 (0.083)	17.8
Euarchonta	18 (0.062)	21.0	17 (0.058)	24.0
Eulipotyphla	24 (0.086)	4.9	24 (0.086)	13.0
Hystricomorpha	2 (0.012)	2.4	1 (0.006)	7.8
Lagomorpha	1 (0.014)	1.9	2 (0.029)	4.4
Marsupialia	17 (0.067)	36.4	7 (0.027)	19.8
Myomorpha + Anomaluromorpha	69 (0.073)	22.2	59 (0.063)	20.8
Sciuromorpha	16 (0.078)	13.4	14 (0.068)	19.3

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Table S2. Selection strength (α) and phylogenetic half-life ($t_{1/2}$) for multi optimum Ornstein-Uhlenbeck (OU) models of trait evolution for carnivory and dietary specialization in mammalian clades. Zero values for α in carnivory or dietary specialization indicates evolution under Brownian Motion (BM) in that clade and phylogenetic half-life was not calculated for that trait. α, selection strength; σ^2, variance rate; $Rt_{1/2}$, relative phylogenetic half-life (represented as percentage of clade's tree height); $At_{1/2}$, absolute phylogenetic half-life in Myr

	Carnivory			Dietary Specialization		
Clade	α	$Rt_{1/2}$ (%)	$At_{1/2}$ (Myr)	α	$Rt_{1/2}$ (%)	$At_{1/2}$ (Myr)
Artiodactyla + Perissodactyla	28.17	2.46	1.17	774.57	0.09	0.04
Atlantogenata	2.59	26.74	20.49	5.30	13.07	10.02
Carnivora + Pholidota	16.51	4.20	1.85	13.80	5.02	2.22
Castorimorpha	0.00	NA	NA	1.46	47.53	22.50
Chiroptera	45.83	1.51	0.62	747.57	0.09	0.04
Euarchonta	54.79	1.26	0.83	14.08	4.92	3.22
Eulipotyphla	12.79	5.42	3.30	165.43	0.42	0.25
Hystricomorpha	7.21	9.61	4.70	0.00	NA	NA
Lagomorpha	359.58	0.19	0.09	0.00	NA	NA
Marsupialia	2.09	33.10	27.37	4.34	15.98	13.22
Monotremata	0.00	NA	NA	0.00	NA	NA
Myomorpha + Anomaluromorpha	1263.23	0.05	0.03	944.29	0.07	0.04
Sciuromorpha	0.00	NA	NA	0.72	96.79	38.91

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Table S3. Contingency table of categorical diet classifications from Price *et al.* (2012) and this study. The diet groupings of Price *et al.* (2012) were reused and pruned to species included in this study (Price categorization). The classification method of Price *et al.* (2012) was replicated using EltonTraits data, where 0% animal matter = herbivore, 1-99% = omnivore, and 100% = carnivore (Strict categorization).

	Price		
Strict	Herbivore	Omnivore	Carnivore
Herbivore	441	63	1
Omnivore	134	250	35
Carnivore	1	34	364

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Supplementary Figures

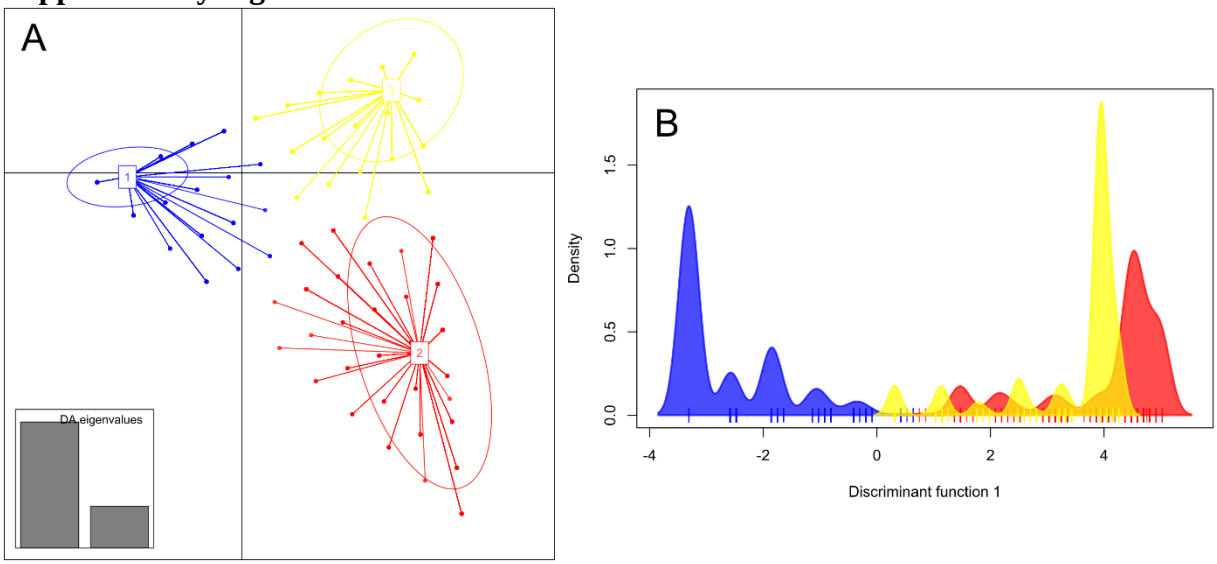


Figure S1. DAPC plot for construction of the degree of carnivory measure. Blue cluster = herbivore, red = vertivore, yellow = invertivore. (A) Distribution of clusters on first and second discriminant functions. (B) Distribution of herbivores, vertivores, and invertivores along the first discriminant function, which was later rescaled to produce the degree of carnivory variable.

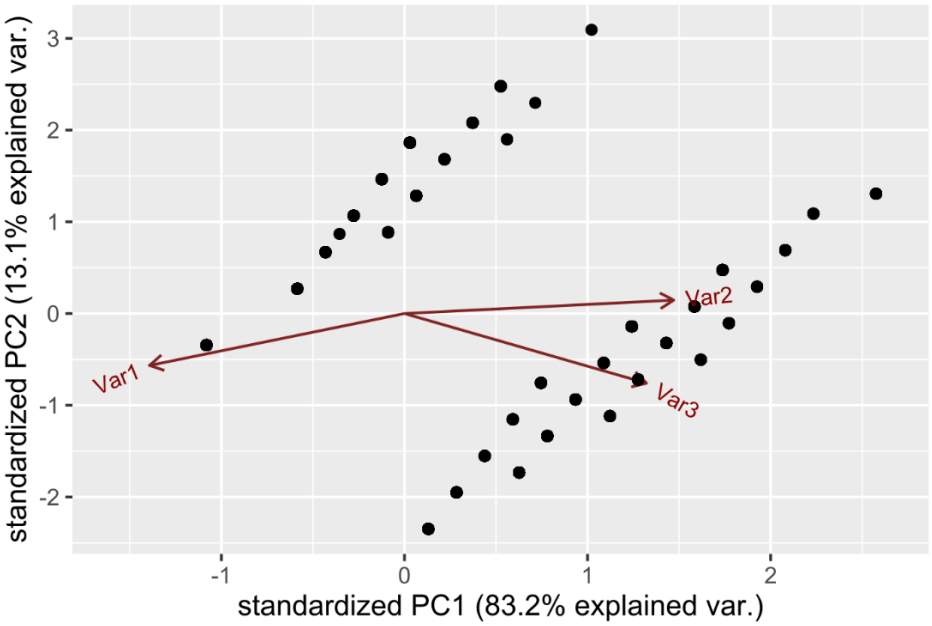


Figure S2. PCA of variables used to construct degree of dietary specialization measure. Scores on PC1 were later rescaled to produce the final dietary specialization variable. Var1 = percentage (from 20 – 100%) of a species' most common food type. Var2 = number of food types (from 1 – 6) included in each species' diet. Var3 = trophic breadth: species that consumed only plants or animals had a score of 1, those that consumed both food types had a score of 2.

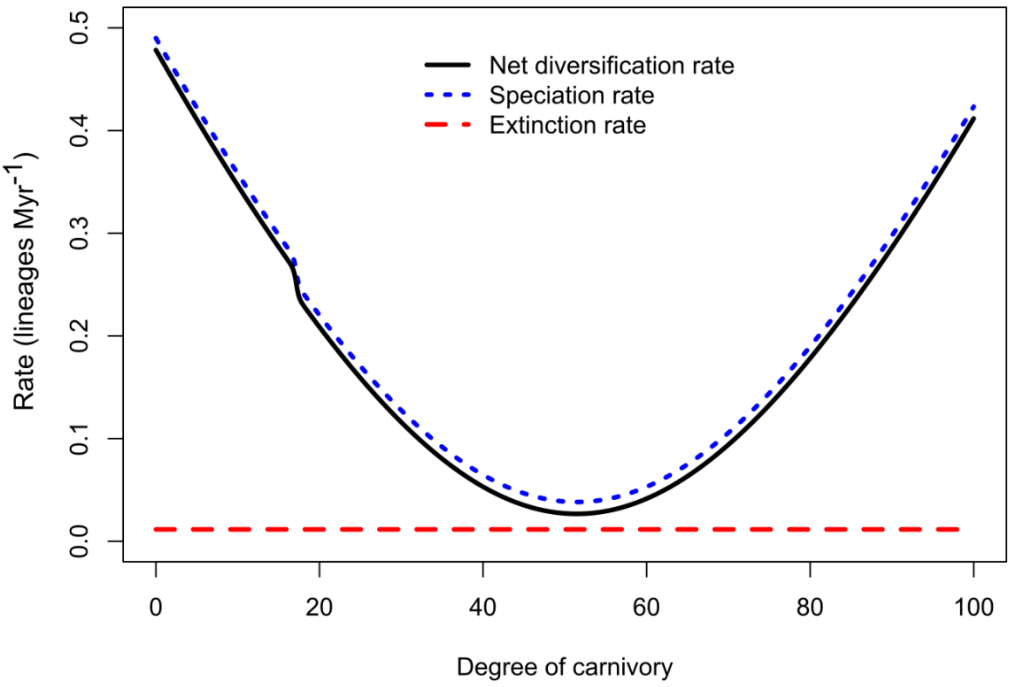


Figure S3. The relationship between degree of carnivory and speciation, extinction, and net diversification rates in Mammalia. The speciation, extinction, and net diversification rate lines represent the relationship produced by averaging over the significant QuaSSE models associated with the eleven phylogenies included in this study.

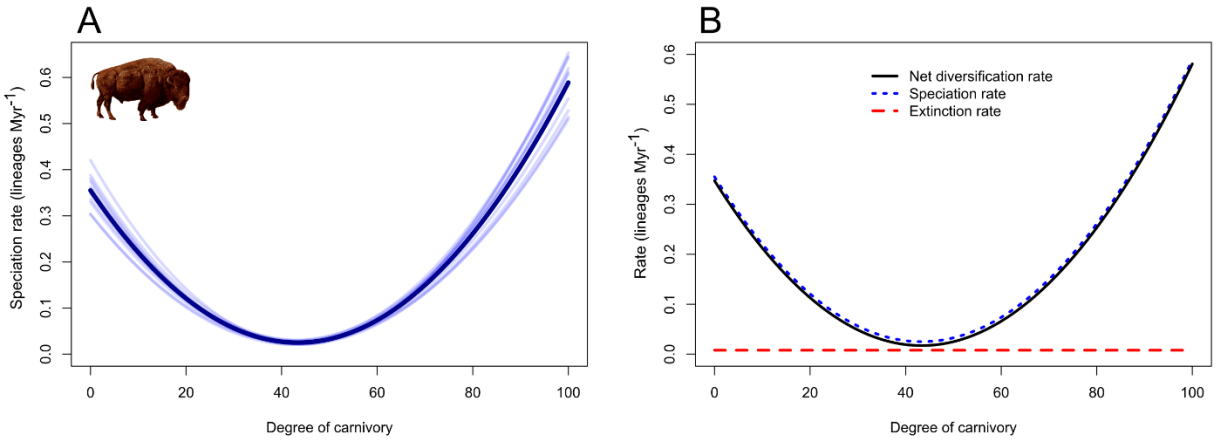


Figure S4. The relationship between degree of carnivory and speciation, extinction, and net diversification rate in Artiodactyla + Perissodactyla. Across the eleven trees used in this study, eleven were associated with a statistically significant best-fitting QuaSSE model in Artiodactyla + Perissodactyla. (A) The transparent blue lines show the relationships between degree of carnivory and speciation rate predicted by these models. The dark blue line represents the relationship produced by averaging over each significant model. (B) The speciation, extinction, and net diversification rate lines represent the relationship produced by averaging over the significant QuaSSE models. Image source: Wikimedia Commons.

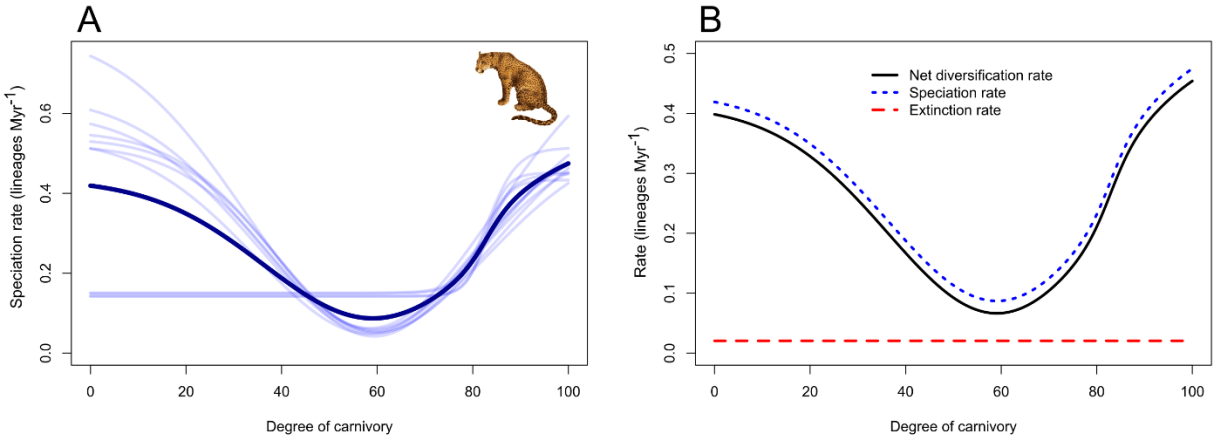


Figure S5. The relationship between degree of carnivory and speciation, extinction, and net diversification rate in Carnivora + Pholidota. Across the eleven trees used in this study, eleven were associated with a statistically significant best-fitting QuaSSE model in Carnivora + Pholidota. (A) The transparent blue lines show the relationships between degree of carnivory and speciation rate predicted by these models. The dark blue line represents the relationship produced by averaging over each significant model. (B) The speciation, extinction, and net diversification rate lines represent the relationship produced by averaging over the significant QuaSSE models. Image source: Wikimedia Commons.

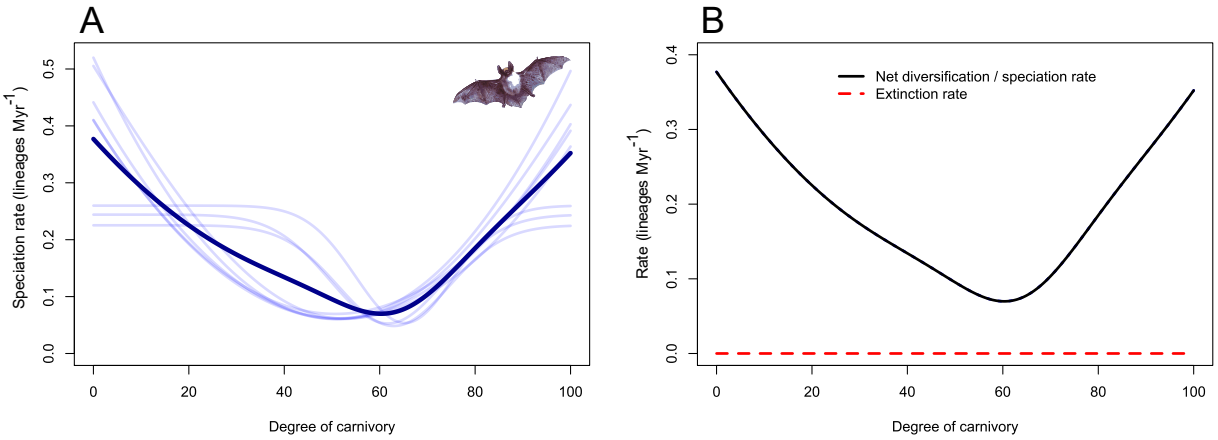


Figure S6. The relationship between degree of carnivory and speciation, extinction, and net diversification rate in Chiroptera. Across the eleven trees used in this study, eight were associated with a statistically significant best-fitting QuaSSE model in Chiroptera. (A) The transparent blue lines show the relationships between degree of carnivory and speciation rate predicted by these models. The dark blue line represents the relationship produced by averaging over each significant model. (B) The extinction and net diversification rate lines represent the relationship produced by averaging over the significant QuaSSE models. Extinction rate was at a constant low level; thus, the speciation and net diversification rates were indistinguishable. Image source: Wikimedia Commons.

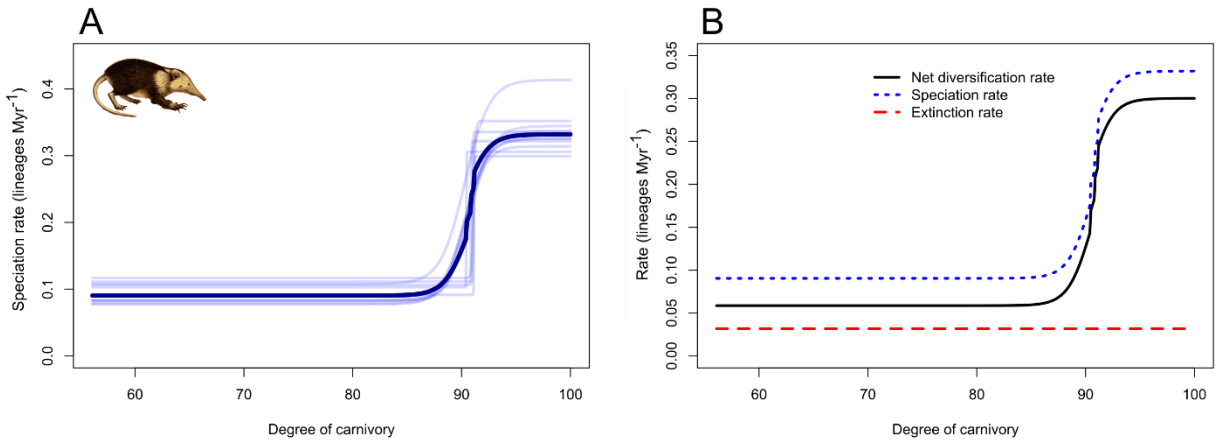


Figure S7. The relationship between degree of carnivory and speciation, extinction, and net diversification rate in Eulipotyphla. Across the eleven trees used in this study, nine were associated with a statistically significant best-fitting QuaSSE model in Eulipotyphla. (A) The transparent blue lines show the relationships between degree of carnivory and speciation rate predicted by these models. The dark blue line represents the relationship produced by averaging over each significant model. (B) The speciation, extinction, and net diversification rate lines represent the relationship produced by averaging over the significant QuaSSE models. Image source: Wikimedia Commons.

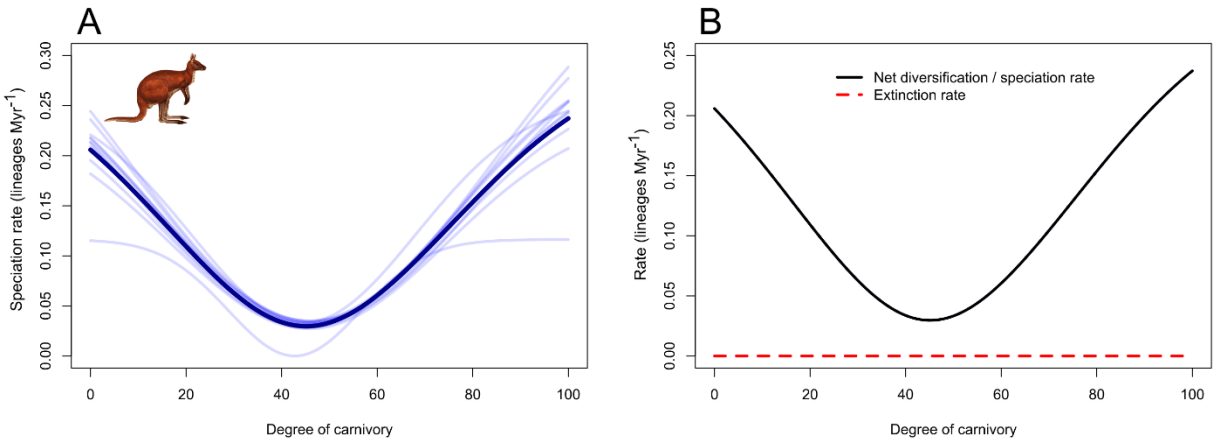


Figure S8. The relationship between degree of carnivory and speciation, extinction, and net diversification rate in Marsupialia. Across the eleven trees used in this study, eleven were associated with a statistically significant best-fitting QuaSSE model in Marsupialia. (A) The transparent blue lines show the relationships between degree of carnivory and speciation rate predicted by these models. The dark blue line represents the relationship produced by averaging over each significant model. (B) The extinction and net diversification rate lines represent the relationship produced by averaging over the significant QuaSSE models. Extinction rate was at a constant low level; thus, the speciation and net diversification rates were indistinguishable. Image source: Wikimedia Commons.

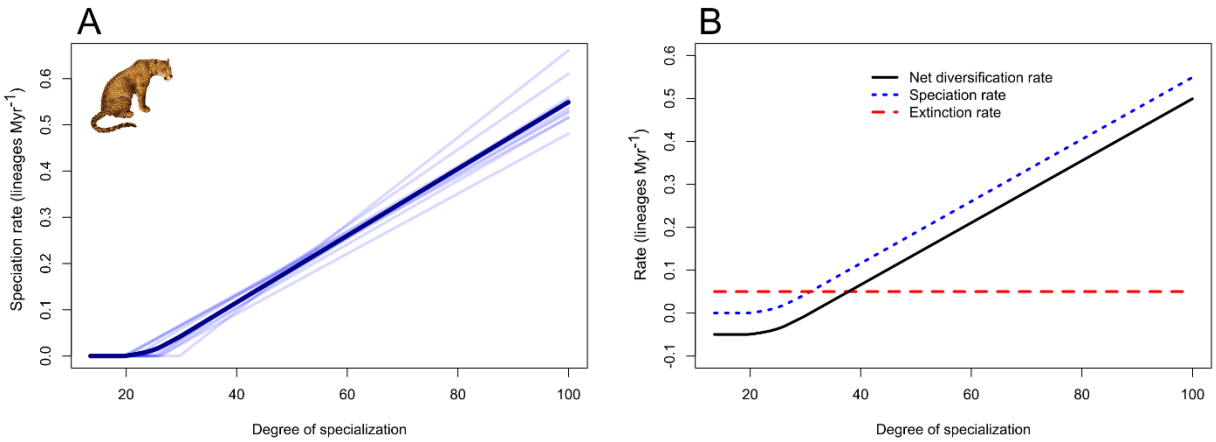


Figure S9. The relationship between degree of dietary specialization and speciation, extinction, and net diversification rate in Carnivora. Across the eleven trees used in this study, eleven were associated with a statistically significant best-fitting QuaSSE model in Carnivora. (A) The transparent blue lines show the relationships between degree of dietary specialization and speciation rate predicted by these models. The dark blue line represents the relationship produced by averaging over each significant model. (B) The speciation, extinction, and net diversification rate lines represent the relationship produced by averaging over the significant QuaSSE models. Image source: Wikimedia Commons.

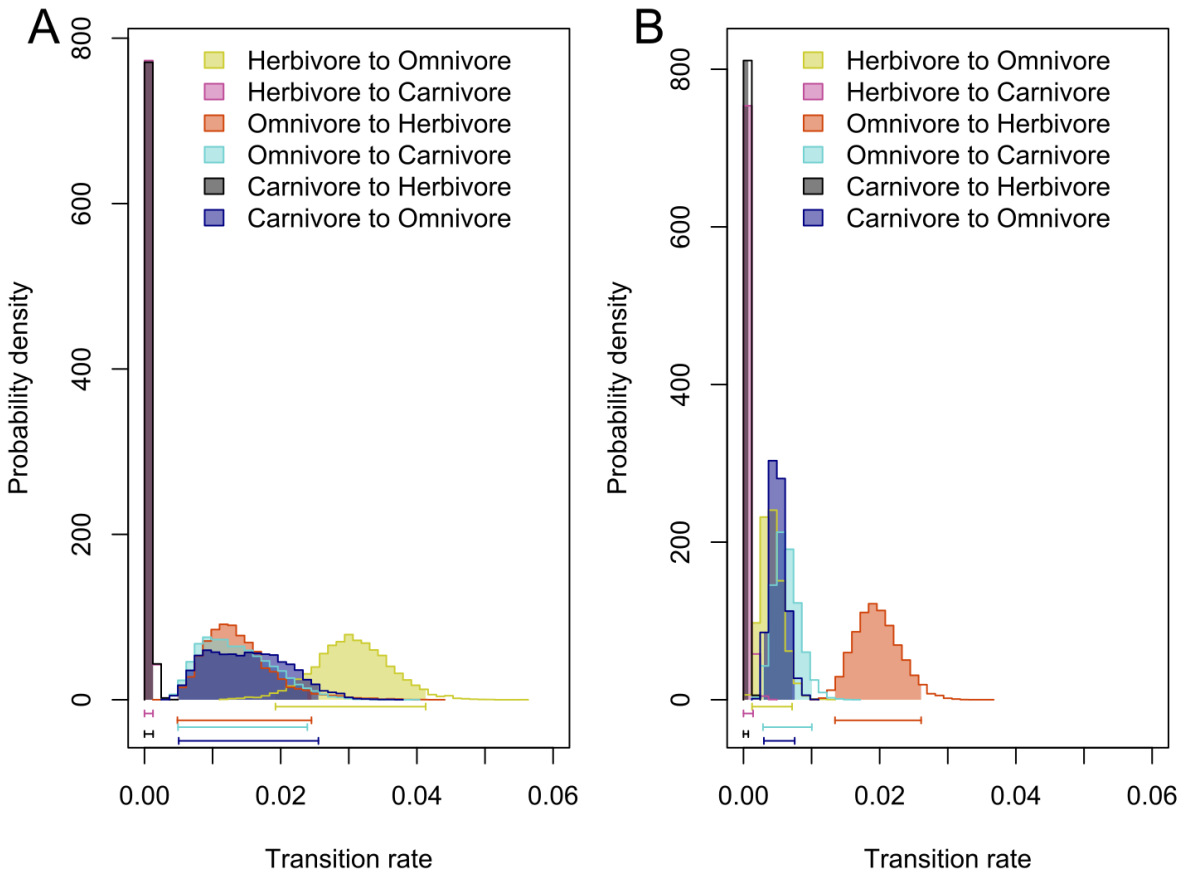


Figure S10. Posterior probability densities for transition rates between herbivores, omnivores, and carnivores, using three diet classification schemes. (A) The diet groupings of Price *et al.* (2012) were reused with the most recent mammalian phylogeny (Upham *et al.* 2019). (B) The classification method of Price *et al.* (2012) was replicated using data from EltonTraits.

Dietary regimes in Carnivora + Pholidota

Within Carnivora, the original carnivory regime was one of moderately high carnivory, with an optimum carnivory score indicative of a diet comprising 80-90% animal matter (Fig. S1). Occupancy of this regime is shared with the pangolins, Pholidota. Contemporary carnivoran clades that still have members in this original carnivory regime include Mephitidae, Canidae, Viverridae, Herpestidae, Eupleridae, and Hyaenidae. A shift towards a similar carnivory regime occurred at the origin of Mustelidae and is still occupied by members of Helictidinae, Guloninae, Mellivorinae, and Taxidiinae. Four independent shifts towards hypercarnivory occurred in Carnivora, including in: Felinae, Pinnipedia, the branch leading to Mustelinae, Ictonychinae, and Lutrinae, and the branch leading to *Ursus maritimus*. Shifts towards varying degrees of herbivory occurred throughout Carnivora. A shift to mesoherbivory occurred in Musteloidea and is still occupied by *Ailurus fulgens* and members of Procyonidae. Similar shifts occurred in Nandiniidae and in Genettinae at the branch leading to *Poiana richardsonii*. There was a shift to hyperherbivory at the origin of Ursidae, followed by a shift to omnivory at the origin of Ursinae, then a subsequent shift to mesoherbivory at the branch leading to *Ursus*. Other shifts to omnivory occurred in Melinae, *Procyon*, Paradoxurinae, *Urocyon*, and the branch leading to *Vulpes cana*.

Fewer regime shifts occurred in Carnivora for degree of dietary specialization. The original score of the regime occupied at the origin of Carnivora was one of intermediate dietary specialization (Fig. S1). The original optimum specialization score is indicative of diets comprising two food types, one animal-based and one plant-based, and an extreme bias toward one of the two food types. Most members of Carnivora still occupy this original specialization regime. Occupancy of this regime is shared with the pangolins, Pholidota. Shifts towards high dietary specialization occurred in Felinae, Genettinae, the branch leading to *Ursus maritimus*, the branch leading to *Speothos venaticus*, and the branch leading to Mustelinae, Ictonychinae, and Lutrinae. Shifts to slightly lower optimum dietary specialization scores occurred at the origin of Viverridae, at the origin of Musteloidea, and at the branch leading to *Mustela itatsi*.

Discussion

Mesocarnivory has previously been reported as the basal condition in Carnivora (Van Valkenburgh 2007; Slater and Friscia 2019). However, our study reported a high optimal degree of carnivory at the origin of Carnivora, suggesting disagreement with previous findings. Earlier studies only considered the proportion of vertebrates in a given species' diet when measuring carnivory (Van Valkenburgh 1988, 2007), whereas we also incorporated invertivory into our carnivory variable. Thus, invertivorous species are considered to have higher degrees of carnivory in this study than they were previously. Extant species with similar carnivory scores to the original optimum value found in this study are predominantly invertivorous and would be considered mesocarnivorous by earlier metrics. Therefore, the optimum degree of carnivory found at the origin of Carnivora supports the findings of earlier studies.

The placement of ecomorphological shifts within Carnivora by Slater and Friscia (2019) is in loose agreement with the results of our study. Whereas the ancestral regime in our analysis extends to include Mephitidae, the earlier study instead reports a shift to omnivory near the base of Caniformia (excluding Canidae). Also, fewer shifts within Feliformia occur in our results. Additional shifts at lower taxonomic levels occur in our study – for example within Ursidae and Canidae – which do not occur in Slater and Friscia (2019). It is unclear if our results contradict their conclusion that there was an early burst in the evolution of dietary strategy within Carnivora.

Carnivora + Pholidota was the only subclade in our analysis to return a significant trait-dependent speciation dynamic for both degree of carnivory and degree of dietary specialization. Carnivoran speciation favored increased specialization for either end of the carnivory spectrum. An evolutionary trend of increasing body size over time, known as Cope's Rule, is documented in Carnivora, as well as in other mammalian lineages (Alroy 1998). Within Carnivora, there is an association between increasing body size and specialization for hypercarnivory (Van Valkenburgh *et al.* 2004). This, in combination with the high energy content and easy digestibility of a carnivorous diet, has been posited as the reason for a bias towards evolution of hypercarnivorous feeding strategies in the carnivoran fossil record (Van Valkenburgh 2007). Increased vulnerability to extinction and reduced species duration of hypercarnivorous lineages has resulted in the repeated appearance of convergent carnivorous forms in distantly related species throughout Carnivora (Van Valkenburgh 1991, 2007; Balisi *et al.* 2018). This evolutionary trend favoring specialization for hypercarnivory explains the positive relationship between increasing degrees of carnivory and speciation rate observed for Carnivora in our analyses.

A positive relationship between hyperherbivory and speciation rate is surprising and is not explained using the same trend. This relationship may instead be driven by the dietary specialization-dependent speciation dynamic observed in Carnivora. Indeed, dietary specialization may play a more important role in the evolution of Carnivora than degree of carnivory, facilitating diversification of herbivorous carnivoran lineages when they arise. Constraints may be placed on the evolution of herbivorous carnivorans due necessarily to their descent from carnivorous ancestors (Figueirido *et al.* 2010), which can explain why shifts to herbivory are infrequent in the order despite the potential for herbivores to speciate quickly.

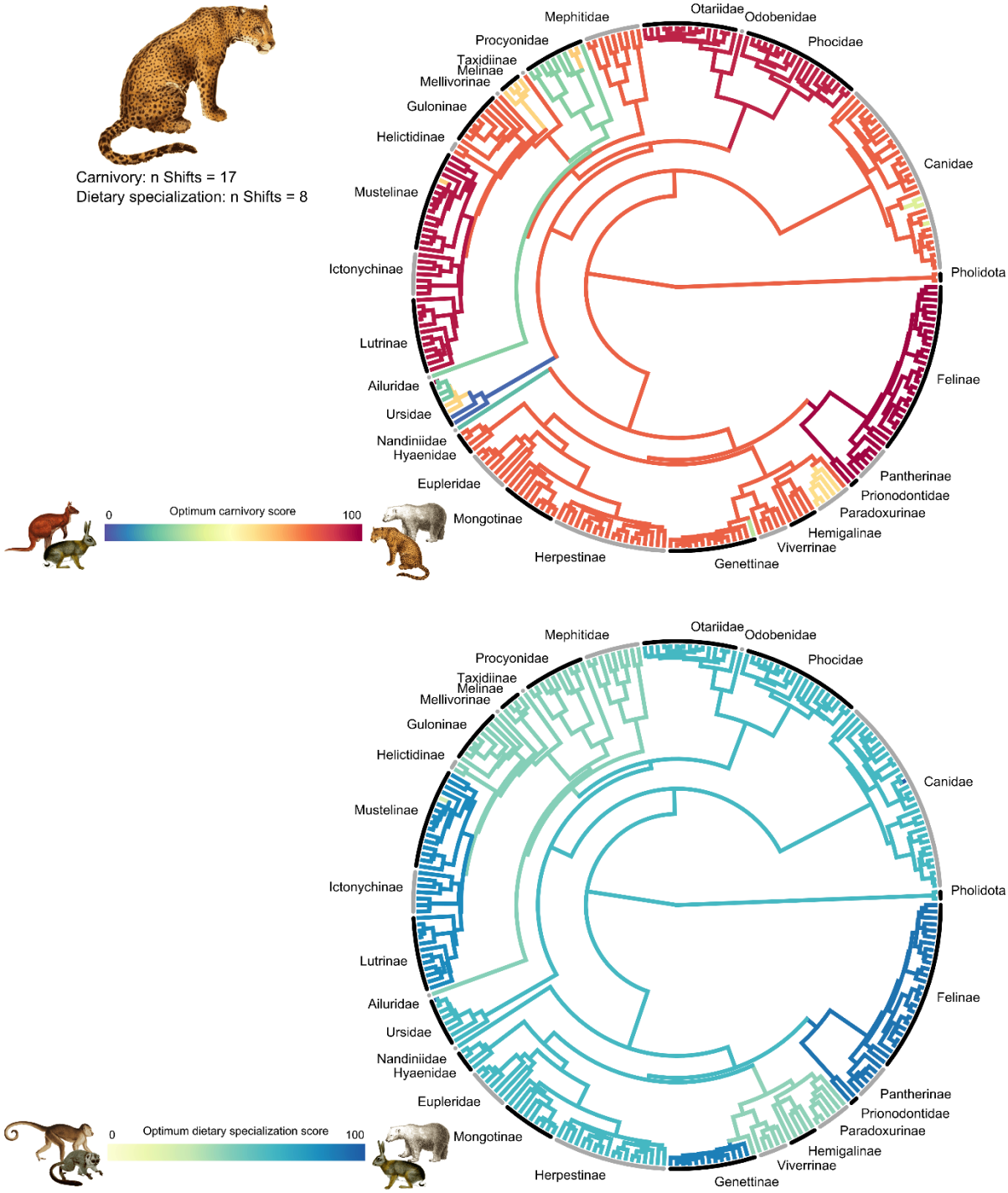


Figure S11. Regime shifts in optimum carnivory score (top) and optimum dietary specialization score (bottom) in Carnivora + Pholidota. Branch color indicates the value of the optimum diet score. Position of color changes represents the location of regime shifts**.** Images source: Wikimedia Commons.

Dietary regimes in Artiodactyla + Perissodactyla

The optimum carnivory score for the regime occupied at the origin of Artiodactyla + Perissodactyla was zero, representing a completely herbivorous diet (Fig. S2). This hyperherbivorous regime is still occupied by all perissodactyls and most artiodactyls. One shift towards hypercarnivory occurred in the branch leading to Cetacea. Following this, multiple descendant shifts within Cetacea occurred, but the changes in optimum carnivory score were small, as all regimes show scores indicative of hypercarnivory. A shift to slightly decreased herbivory occurred at the origin of Cephalophinae and another occurred at the origin of Suina. Following this shift in Suina, shifts toward mesoherbivory occurred at the branch leading to *Sus* and *Potamochoerus*, the branch leading to *Babyrousa celebensis*, and the branch leading to *Pecari* and *Tayassu*. Some shifts within Suina reverted to an optimum carnivory score indicative of complete herbivory: one in the branch leading to *Babyrousa babyrussa*, one in the branch leading to *Hylochoerus meinertzhageni*, and one in the branch leading to *Catagonus wagneri*.

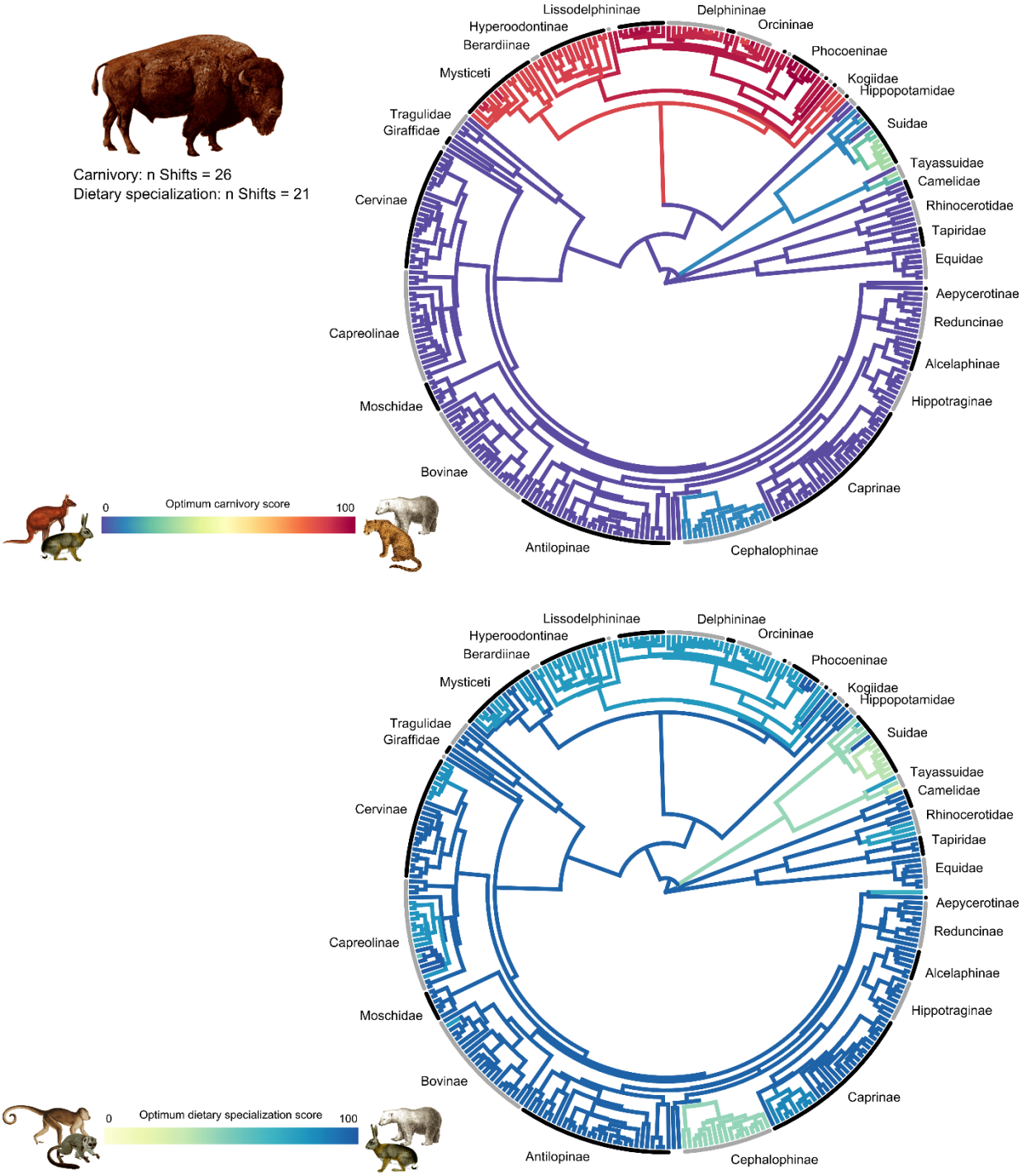
The optimum degree of dietary specialization at the origin of Artiodactyla + Perissodactyla was high, representing specialization on a single food type (Fig. S2). Shifts to a slightly lower degree of specialization – indicative of a diet comprising two food types that are both plant-based or both animal-based, with a bias towards one food type over the other – occurred at many points across Artiodactyla + Perissodactyla: in Odontoceti (minus Kogiidae and Physeteridae), in the branch leading to *Eschrichtius*, *Balaenoptera*, and *Megaptera*, in *Muntiacus*, in Rangiferini (minus *Rangifer*), in *Taurotragus*, in the branch leading to *Naemorhedus* and *Capricornis*, in *Neotragus*, in the branch leading to *Rhinoceros* and *Dicerorhinus*, in *Catagonus*, and in the branch leading to *Babyrousa babyrussa*. Shifts even further towards dietary generalism occurred at the origins of Cephalophinae and Suina. Following the shift in Suina, an additional shift back to complete dietary specialization occurred in the branch leading to *Hylochoerus meinertzhageni*.

Discussion

Most artiodactylan shifts in optimum degree of carnivory occur within Cetacea. Cetaceans include the filter-feeding, primarily zooplanktivorous mysticetes and the fish- or squid-feeders within Odontoceti. Our variable representing degree of carnivory attributes slightly different weights to invertivory and vertivory. Thus, the optimum carnivory score of cetaceans, especially odontocetes, varies frequently as the proportion of fish (vertebrates) and squid (invertebrates) in a given species' diet differs between taxa. While there is variation in the types of plant matter consumed by non-cetacean ungulates, most are still completely herbivorous, so few regime shifts in degree of carnivory could occur. Although there is little evidence for a rapid adaptive radiation within Cetacea (Steeman *et al.* 2009; Slater *et al.* 2010), extant whales represent a relatively speciose clade compared to some other ungulate groups. This is especially true in comparison to clades with omnivorous members, which are restricted to the smaller Suina suborder. This would explain the significant relationship between degree of carnivory and speciation rate observed for Artiodactyla + Perissodactyla, where herbivores and carnivores have higher speciation rates than more omnivorous species.

Shifts in dietary specialization were more evenly distributed across Artiodactyla + Perissodactyla. However, apart from in Suina and Cephalophinae, most of these regime shifts maintained relatively high optimum specialization scores. There was no significant relationship between degree of dietary specialization and speciation rate in Artiodactyla + Perissodactyla. Generalist, mixed-feeders were previously shown to have higher diversification rates than browse-specialist

ruminants (Cantalapiedra *et al.* 2014). However, specialist grazers also had higher diversification rates than browse-specialists, indicating that there is not a strictly dietary specialization-dependent diversification dynamic occurring within Artiodactyla. Additionally, browsers, grazers, and mixed-feeders are all scored as folivore specialists in our study, meaning that this diversification dynamic cannot be captured using our variable. Studies assessing diet at different levels of coarseness detect different relationships between diet and diversification. These studies are complementary to one another and it is important to continue assessing at different scales to elucidate the full picture of diet-dependent diversification across different taxa.



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228 **Figure S12.** Regime shifts in optimum carnivory score (top) and optimum dietary specialization
229 score (bottom) in Artiodactyla + Perissodactyla. Branch color indicates the value of the optimum
230 diet score. Position of color changes represents the location of regime shifts. Images source:
231 Wikimedia Commons.

Dietary regimes in Chiroptera

The carnivory regime occupied at the origin of Chiroptera had an optimal carnivory score similar to extant species whose diets are comprised exclusively of invertebrates (Fig. S3). All chiropteran families have members that still occupy this original regime, excluding Pteropodidae and Phyllostomidae. Most regime shifts in degree of carnivory and dietary specialization occur in Phyllostomidae; shifts were infrequent throughout the rest of Chiroptera.

Regime shifts to an optimum carnivory value representing a completely herbivorous diet occurred at the origin of Pteropodidae and throughout Phyllostomidae, specifically in the branch leading to Carolliinae, throughout Stenodermatinae, and in the branch leading to *Lichonycteris*. Regimes with slightly reduced degrees of hyperherbivory occur in Rousettinae, Phyllostominae, Stenodermatinae, and Glossophaginae. Regimes with optimum diets suggesting mesoherbivory occur only within Phyllostomidae: in Glossphaginae, Lochophyllinae, Stenodermatinae, and Phyllostominae. Multiple shifts to mesocarnivory occurred in Chiroptera: throughout Rhinolophidae, at the branch leading to *Emballonura* and *Paremballonura*, and at the origin of Phyllostomidae. Additional shifts to mesocarnivory occurred within Phyllostomidae, specifically within Glyphonycterinae, Phyllostominae, and Micronycterinae. Regimes with optimum carnivory scores indicative of omnivorous diets are rare and originated in the branches leading to *Macrotus* and *Mimon*. Shifts where the optimum diet showed an increase in carnivory indicative of vertivory occurred within Megadermatidae, within *Nycteris*, and at the origin of Desmodontinae.

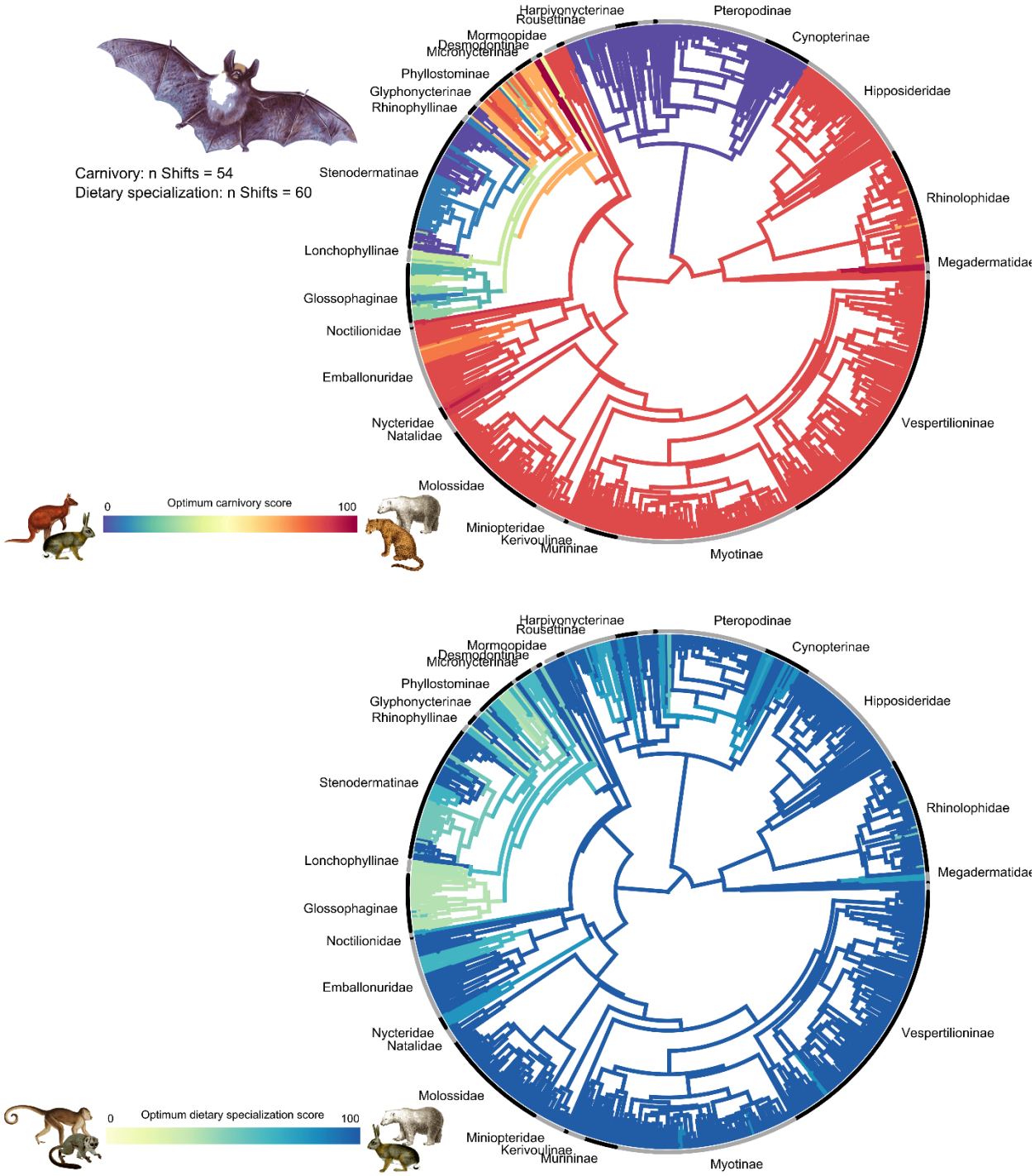
The optimum degree of dietary specialization at the origin of Chiroptera was one of complete specialization (Fig. S3). Except for Phyllostomidae, all chiropteran families still have members included in this original regime. Across Chiroptera, there were multiple shifts to optimum specialization values indicative of a diet comprising two different food types, but with a bias towards one type. These occurred within Noctilionidae, within Megadermatidae, within *Myotis*, at the branch leading to Nycteridae, throughout Pteropodidae, and in the branch leading to *Antrozous* and *Bauerus*. There were several shifts to optimum specialization scores indicative of moderately generalized diets comprising three or more different food types, both plant- and animal-based. These occurred throughout Phyllostomidae, but also within Emballuronidae, Pteropodidae, and Rhinolophidae. Regime shifts back to complete dietary specialization occurred throughout Pteropodidae and Phyllostomidae, specifically within Cynopterinae, Pteropodinae, Rousettinae, Desmodontinae, Lonchorhininae, Phyllostominae, Carolliinae, and Stenodermatinae.

Discussion

Invertivory was the basal condition in Chiroptera, reinforcing the consensus that the common ancestor was insectivorous (Gunnell and Simmons 2005). Our results show that the optimal diet at the origin of Phyllostomidae – the clade with most dietary diversity (Freeman 2000) – was mesocarnivorous. Previous findings reported that the ancestral diet of Phyllostomidae was insectivorous (Datzmann *et al.* 2010). However, our study indicated that regime shifts in degrees of carnivory and dietary specialization occurred at the origin of the family. These shifts were associated with an optimal diet that, although primarily still carnivorous, showed a decrease in dietary specialization in favor of increasing herbivory. Our findings align with recent studies that identified molecular adaptations for processing diverse macronutrients (Potter *et al.* 2021) and development of an omnivorous sensory morphotype (Hall *et al.* 2021) on the branch leading to Phyllostomidae. These results suggest that the ancestral phyllostomid diet was relatively generalized and that the foundation for phyllostomid dietary diversity was laid at its origin.

We observed a significant relationship between speciation rate and degree of carnivory in Chiroptera. Although the majority of extant bats are reported to be united by a single diversification process (Shi and Rabosky 2015), shifts in diversification rate have been inferred within chiropteran clades (Jones *et al.* 2005) and some of these have been attributed to changes in feeding strategy (Dumont *et al.* 2011; Monteiro and Nogueira 2011). We found that speciation rates are highest at either extreme end of the carnivory score spectrum, with omnivorous and mesocarnivorous species having the lowest rates (Fig. S6). Carnivorous diets predominate in Chiroptera and hyperherbivory is prevalent in two diverse chiropteran clades – Phyllostomidae and Pteropodidae. Conversely, omnivorous and mesocarnivorous chiropterans are comparatively rare, existing in small numbers primarily within Phyllostomidae. Thus, the distribution of carnivory scores across Chiroptera is consistent with the relationship between degree of carnivory and speciation rate that we detected.

We did not observe a significant relationship between degree of dietary specialization and speciation rate in Chiroptera. This result is perhaps unsurprising, given that earlier studies of dietary specialization's impact on chiropteran diversification have reached contradicting conclusions. Specialization for frugivory has been implicated as a cause for increased diversification in Neotropical noctilionoid bats (Rojas *et al.* 2012). However, a more recent study of noctilionoid bats reported that generalist herbivores speciate faster than specialized herbivores (Rojas *et al.* 2018). Our study examined the taxonomic breadth of Chiroptera and assessed the impact of dietary specialization independently of degree of carnivory. So, dietary specialization-dependent speciation dynamics may exist within smaller subsets of Chiroptera, but these relationships are not representative of all bats or diet types.



297

298 **Figure S13.** Regime shifts in optimum carnivory score (top) and optimum dietary specialization
299 score (bottom) in Chiroptera. Branch color indicates the value of the optimum diet score. Position
300 of color changes represents the location of regime shifts. Images source: Wikimedia Commons.

Dietary regimes in Euarchonta

At the origin of Euarchonta, the optimum carnivory score was one of mesoherbivory (Fig. S4). This regime was occupied during the origin of Primates, but Dermoptera and Scandentia shifted to new regimes with optimum diets suggestive of complete herbivory and high carnivory, respectively. Contemporary members of the original euarchontan carnivory regime still exist within Strepsirrhini, specifically *Perodicticus potto*, *Daubentonia madagascariensis*, and members of Galagidae. Shifts towards optimum diets of hyperherbivory occurred in the branch leading to the Simiiformes and the branch leading to Lemuridae, Cheirogalidae, Lepilemuridae, and Indriidae. Within Simiiformes, subsequent shifts to complete herbivory occurred at the origin of Colobinae and in the branch leading to *Erythrocebus*. Regime shifts back to an optimum diet of mesoherbivory occurred in the branch leading to *Microcebus*, in the branch leading to Cebidae, Callitrichidae, and Aotidae, in the branch leading to *Papio*, and at the origin of Cercopithicini. Multiple regime shifts towards varying degrees of increased carnivory occurred within Strepsirrhini: in the branches leading to *Mirza*, *Paragalago*, *Galagoides*, and *Arctocebus*, and in the branch leading to Lorisinae. There was another shift to an optimal diet of complete carnivory at the origin of Tarsiidae. Independent shifts towards increased omnivory occurred in the branches leading to *Microcebus*, *Macaca fascicularis*, and *Papio anubis*.

The optimum dietary specialization score for the regime occupied at the origin of Euarchonta was 100, representing complete specialization (Fig. S4). Dermoptera and Scandentia still include members of this original regime. A slight decrease in dietary specialization occurred in the branch leading to *Tupaia*. In the branch leading to Primates, there was a regime shift to an optimal dietary specialization score indicative of a diet comprising three different food types, split equally between animal and plant matter. This regime is still occupied by members of Strepsirrhini and Haplorrhini. A similar regime exists within Scandentia, in the branch leading to *Ptilocercus*. Shifts back to increased dietary specialization in Primates took place in the branch leading to Lemuridae, Cheirogalidae, Lepilemuridae, and Indriidae, in the branch leading to *Allocebus*, at the origin of Tarsiidae, and throughout Simiiformes in the branches leading to Alouattinae, *Gorilla*, Colobinae, *Theropithecus*, and the branch leading to *Chlorocebus tantalus* and *C. djamdjamensis*. Regimes with decreased optimum dietary specialization occurred at the origin of Cheirogalidae and the branch leading to Cebidae, Callitrichidae, and Aotidae. Callitrichidae experienced a regime shift back to a similar optimum degree of dietary specialization as observed at the origin of Primates. Members of Cebidae and Aotidae have optimum specialization scores of zero, representative of extreme dietary generalism.

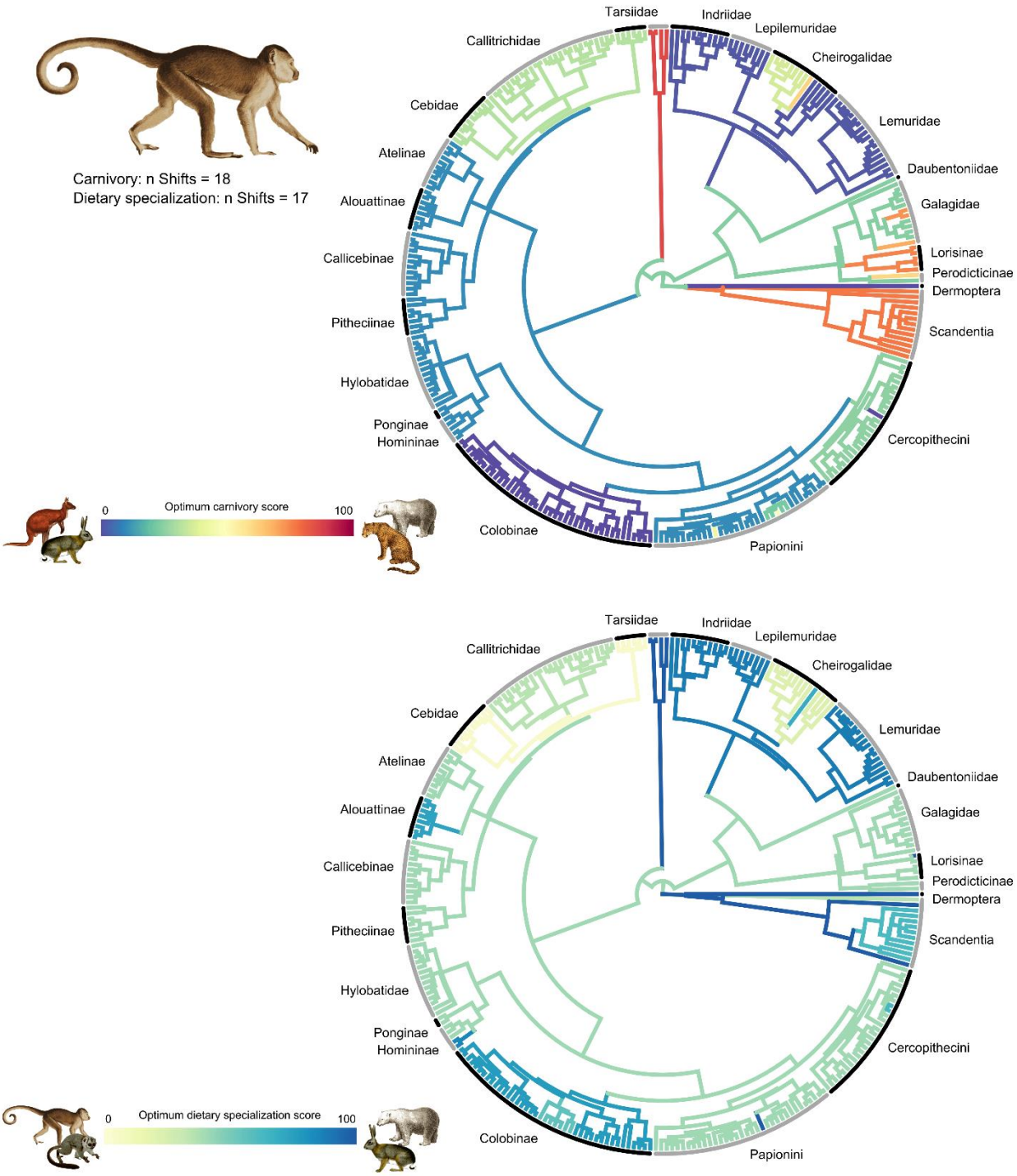
Discussion

It has been suggested that the origin of Primates involved an adaptive shift towards a new feeding strategy, with competing hypotheses that this shift either represented a transition from ancestral insectivory to herbivory (Szalay 1968) or a transition to visual predation on insects in the lower canopy (Cartmill 1974). Our results instead indicate that the primate origin is associated with continued occupancy of the basal euarchontan carnivory regime, with an optimal diet of mesoherbivory. Previous findings that the origin of primates did not involve an adaptive shift in chewing behavior were used to indicate that changes in food acquisition were decoupled from changes in jaw-muscle activity during primate evolution (Vinyard *et al.* 2007). However, those results could instead provide further evidence for the lack of a dietary shift at the origin of Primates.

The basal condition of Euarchonta is contended to be most similar to *Ptilocercus*, considered the most plesiomorphic extant tree shrew (Szalay and Drawhorn 1980). Thus, the ancestral euarchontan was suggested to be predominantly insectivorous like *Ptilocercus* (Bloch *et al.* 2007). This contradicts the results of our regime shift analyses, where a shift to a carnivorous optimum diet arose in Scandentia, from an ancestral mesoherbivorous regime. Our notion of an herbivorous optimal diet at the origin of Euarchonta was supported by reconstruction of ancestral bitter taste receptor (TAS2R) gene numbers within Euarchontoglires (Hayakawa *et al.* 2014). *Tas2r* gene number is positively correlated with the proportion of plant matter in a given species' diet (Li and Zhang 2013). At the origin of Euarchonta, *Tas2r* gene number was high, remained high throughout the evolution of Primates, but decreased with the divergence of the insectivorous Scandentia.

We found no significant relationship between speciation rate and degree of carnivory or degree of dietary specialization in Euarchonta. An earlier study found that primates possessing mutualistic dietary interactions with plants (i.e. frugivores) had higher diversification rates than those with antagonistic interactions (i.e. folivores and insectivores) (Gómez and Verdú 2012). Our measure of degree of carnivory does not differentiate between folivory and frugivory, so both forms of herbivory are attributed the same carnivory score. It would therefore not be possible to observe the same diet-dependent diversification dynamic using our study design. Thus, the results of the two studies do not compete against one another. However, a more recent study showed that insectivorous primate lineages have diversified more slowly than herbivorous lineages (Scott 2019). This diversification dynamic is driven by a low rate of diversification in nocturnal lineages relative to diurnal ones, as there is an association between insectivory and nocturnality in Primates. Reasons for our inability to return the same significant relationship between degree of carnivory and speciation rate may include our use of a continuous variable instead of categorical one, or by expansion of our trait-dependent speciation analyses to all euarchontans.

Lack of an observable relationship between dietary specialization and speciation rate in Euarchonta corroborates previous findings. Specialization for folivory was not related to changes in diversification rate in African colobine monkeys but was shown to depress diversification in Asian colobines (Tran 2014). Primate frugivory-specialist lineages did not show significantly different net diversification rates to non-frugivores (Scott 2018, but see Gómez and Verdú 2012). These results indicate that dietary specialization – measured at either a finer scale as in the previous studies or more broadly as in our study – does not have a significant impact on diversification rate in Euarchonta.



376

377 **Figure S14.** Regime shifts in optimum carnivory score (top) and optimum dietary specialization
378 score (bottom) in Euarchonta. Branch color indicates the value of the optimum diet score. Position
379 of color changes represents the location of regime shifts. Images source: Wikimedia Commons.

Dietary regimes in Eulipotyphla

Within Eulipotyphla, the original carnivory regime had a hypercarnivorous optimum diet (Fig. S5). Numerous shifts in optimum degree of carnivory occur throughout Eulipotyphla. For most of these shifts, the change in optimum carnivory score is small, and the regimes retain a hypercarnivorous optimum value. Exceptions to this include the shifts to mesocarnivory within Erinaceinae and in the branch leading to *Blarina*, and the shift to omnivory in Solenodontidae.

The original optimum dietary specialization score occupied at the origin of Eulipotyphla was consistent with a diet that comprises two different food types, is exclusively animal- or plant-based, and has a bias towards one food type over the other (Fig. S5). As was the case with degree of carnivory, there are numerous shifts in optimum dietary specialization score throughout Eulipotyphla, but with little variation in optimum specialization value. Shifts towards extreme dietary specialization occurred in Galericinae, Talpinae, and in the branches leading to *Anourosorex*, *Notiosorex*, *Ruwenzisorex*, and *Scutisorex*. Shifts to moderate to high dietary generalism occurred within Erinaceinae, Solenodontidae, and in the branch leading to *Blarina*.

Discussion

Although many shifts in both degree of carnivory and degree of dietary specialization were detected throughout Eulipotyphla, most of these regime shifts corresponded to only slight changes in optimum carnivory or dietary specialization scores. Eulipotyphla shows less dietary diversity than many other mammalian clades, as most members are predominantly invertivorous or vertivorous, with some rarer omnivorous members included. The evolution of eulipotyphlan diet is not well studied so there is little to compare our regime shift analyses to. Our results provide support for a previously suggested insectivorous origin for Eulipotyphla (Wu *et al.* 2017). A shift to increased diversification rate was previously reported in a branch leading to *Crocidura*, the most speciose genus within Eulipotyphla (Rossi *et al.* 2018). Members of *Crocidura* are coded as consuming equal proportions of invertebrates and vertebrates in the EltonTraits dataset (Wilman *et al.* 2014), which would increase their carnivory score relative to predominantly invertivorous eulipotyphlans. This could explain the association between extreme hypercarnivory and heightened speciation rate observed for Eulipotyphla in our study.

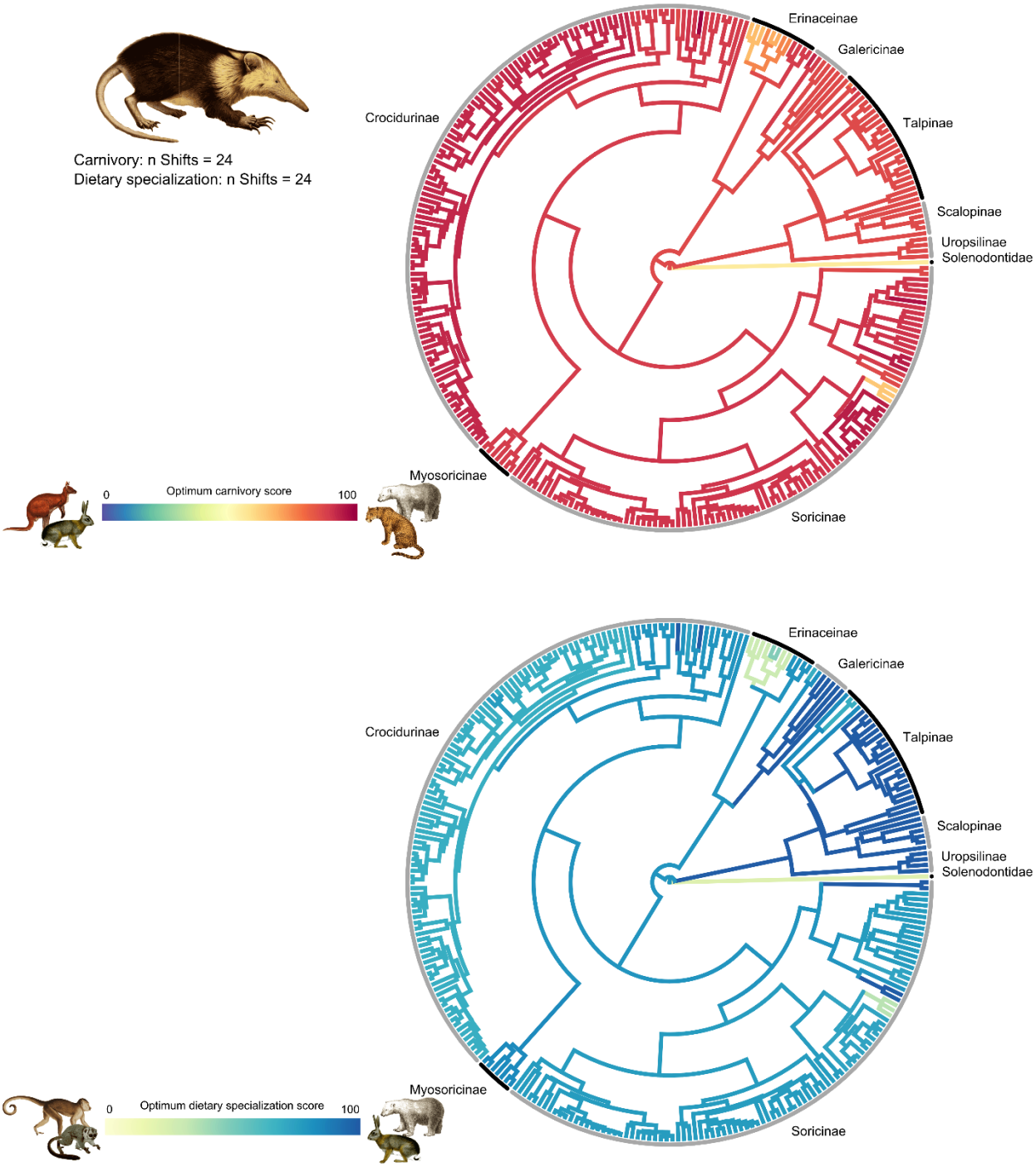


Figure S15. Regime shifts in optimum carnivory score (top) and optimum dietary specialization score (bottom) in Eulipotyphla. Branch color indicates the value of the optimum diet score. Position of color changes represents the location of regime shifts. Images source: Wikimedia Commons.

Dietary regimes in Lagomorpha

Most members of Lagomorpha belong to a single dietary regime for both degree of carnivory and degree of dietary specialization (Fig. S6). The optimum carnivory score for most of Lagomorpha is one of complete herbivory, and the optimum dietary specialization score is one of complete specialization. One regime shift in optimum degree of carnivory occurred in Lagomorpha: a slight increase in carnivory in the branch leading to *Lepus coreanus*, *L. timidus*, and *L. arcticus*. Two shifts in degree of dietary specialization occurred in Lagomorpha. The first represented a shift towards a diet comprising two different herbivorous food types in *Pentalagus furnessi*. The second represented a shift to a diet comprising both plant and animal matter in the branch leading to *Lepus arcticus*.

Discussion

The short phylogenetic half-life of degree of carnivory in Lagomorpha was surprising, given the lack of diversity in diet types within the clade and that dietary specialization evolved under Brownian motion. Within the EltonTraits dietary dataset, all members of Lagomorpha are coded as completely herbivorous, except for *Lepus arcticus*, which has a diet comprising 30% vertebrates (Wilman *et al.* 2014). Arctic hares are known to consume meat occasionally, but they are usually completely herbivorous (Best and Henry 1994). Coding *L. arcticus* as partially meat-eating may have led to an erroneous α value for Lagomorpha in our regime shift analyses, which would otherwise have shown no shift in degree of carnivory. This, in combination with the small size of Lagomorpha, which is known to cause less accurate estimations of phylogenetic half-life (Hansen *et al.* 2008), suggests that this result may be unreliable.

Dietary regimes in Atlantogenata

Few shifts in optimum degree of carnivory or optimum degree of dietary specialization have occurred throughout Atlantogenata (Fig. S7). The optimum carnivory score for most of Atlantogenata is consistent with extant species' diets that show extreme invertivory. There were two shifts towards optimum carnivory scores indicative of complete herbivory: one at the origin of Folivora and another at the origin of Paenungulata. One shift to a mesocarnivorous optimum diet occurred in the branch leading to *Chaetophractus* and *Euphractus*. Two shifts towards omnivory occurred: one in *Echinops telfairi* and the other in *Euphractus sexcinctus*. The optimum degree of dietary specialization for most of Atlantogenata was one of complete specialization. Shifts to varying degrees of increased generalism occurred throughout Atlantogenata: in the branch leading to *Macroscelides*, in the branch leading to *Chaetophractus* and *Euphractus*, in the branch leading to *Tolypeutes*, and in the branch leading to Tenrecinae. There was one shift back to an optimum of complete dietary specialization in the branch leading to *Hemicentetes*.

Discussion

Because the grouping of Afrotheria and Xenarthra into Atlantogenata has historically been contentious (Esselstyn *et al.* 2017; Upham *et al.* 2019), there is a dearth of literature on the evolution of diet within Atlantogenata. The ancestral condition of Xenarthra has been reconstructed as myrmecophagous due to the dramatically reduced dentition observed in xenarthrans, which is usually associated with invertivory (Gaudin and Croft 2015). This agrees with the results of our regime shift analyses. Our results also indicate the ancestral optimal condition of Afrotheria was one of high carnivory, with the common ancestor of Afrotheria sharing the same dietary regime as the common ancestor of Xenarthra.

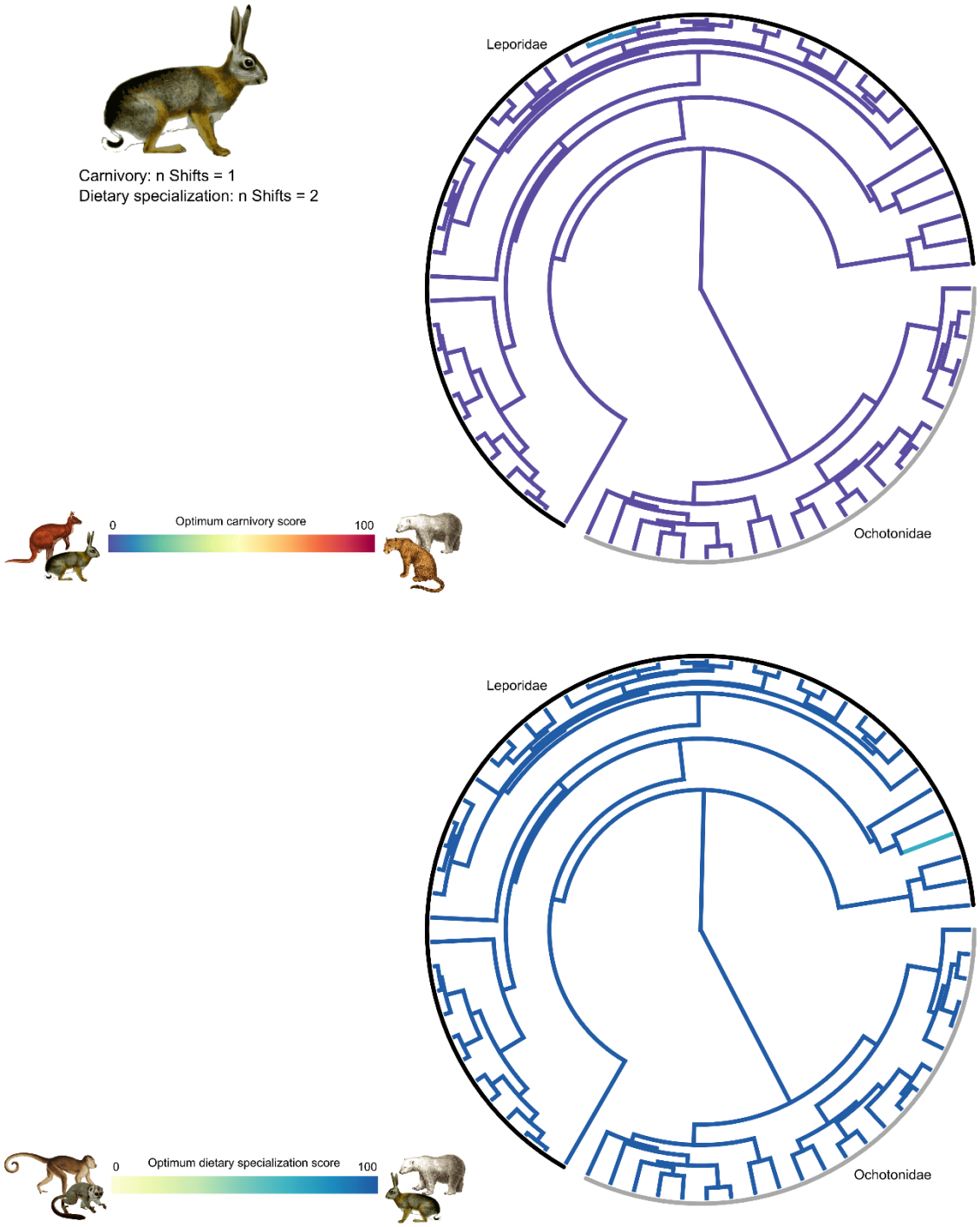


Figure S16. Regime shifts in optimum carnivory score (top) and optimum dietary specialization score (bottom) in Lagomorpha. Branch color indicates the value of the optimum diet score. Position of color changes represents the location of regime shifts. Images source: Wikimedia Commons.

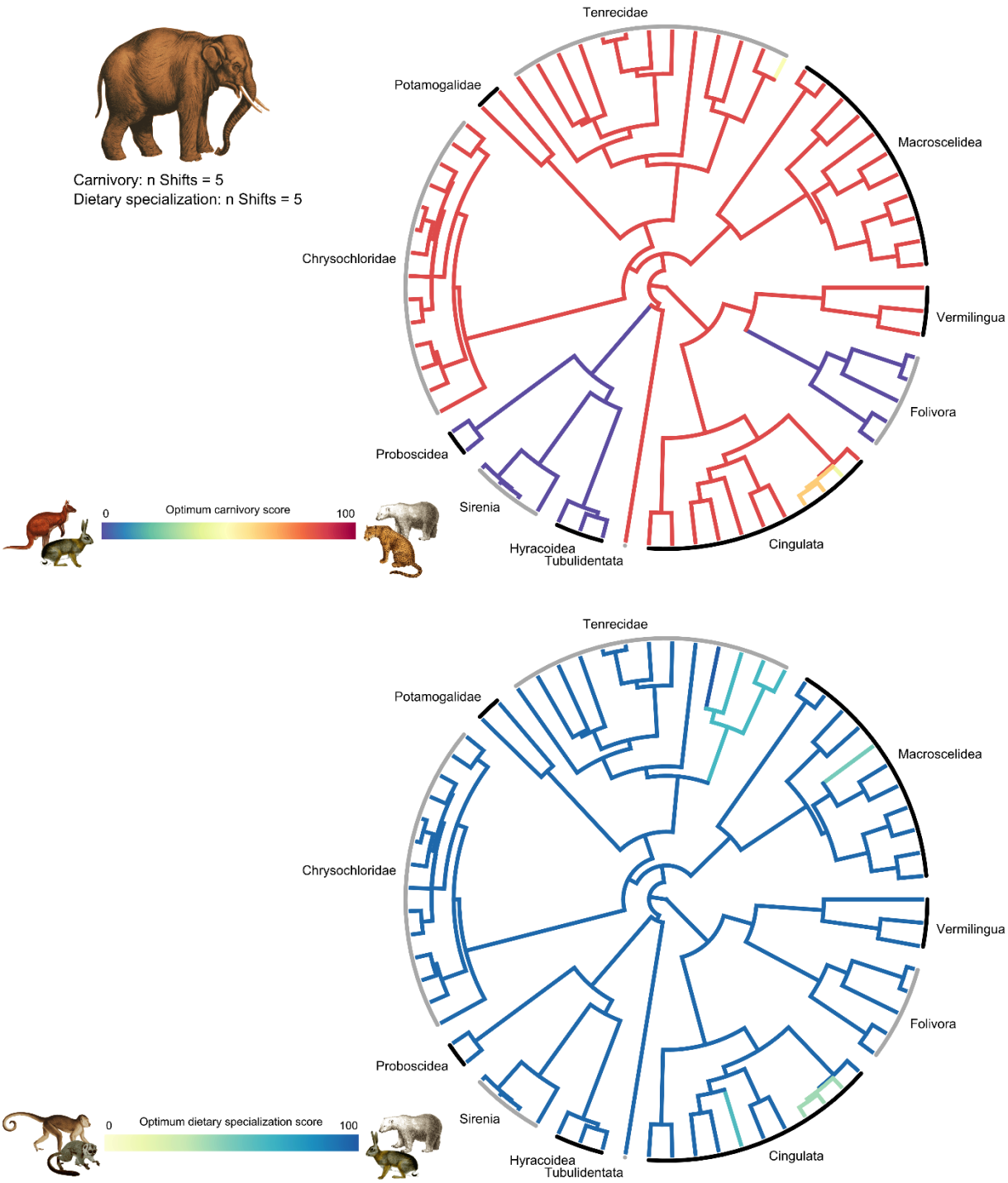


Figure S17. Regime shifts in optimum carnivory score (top) and optimum dietary specialization score (bottom) in Atlantogenata. Branch color indicates the value of the optimum diet score. Position of color changes represents the location of regime shifts. Images source: Wikimedia Commons.

Dietary regimes in Marsupialia

At the origin of Marsupialia, the optimum diet was mesocarnivorous (Fig. S8). This original mesocarnivorous regime is still occupied by Caenolestidae and members of Didelphidae, specifically in Glironiinae, Hyladelphinae, and the Marmosini tribe of Didelphinae. At the origin of Australidephia, there was a regime shift to a hypercarnivorous optimum diet that is consistent with an increase in vertivory. Similar shifts to hypercarnivory occurred within Didelphidae, in the branch leading to *Thylamys* and the branch leading to the tribes Didelphini and Metachirini. A subsequent shift to an optimum diet of hyperherbivory took place at the origin of Diprotodontia. Shifts to omnivory occurred in the branches leading to Thylamyini, Acrobatidae, Petauridae, and Hypsiprymnodontinae, as well as the branch leading to Echymiperinae and Peroryctinae, and the branches leading to *Pseudantechinus bilarni*, *Parantechinus*, and *Phascolosorex*. Regime shifts to an optimum diet of mesoherbivory occurred at the origins of Caluromyinae and Burramyidae. There were two shifts back to mesocarnivory in *Acrobates* and *Dactylopsila*.

Moderate dietary generalism was optimum at the origin of Marsupialia (Fig. S8). The original regime for dietary specialization had an optimum specialization score similar to diets comprising four different food types, but with a strong bias toward a single food type. Similar to the original regime for degree of carnivory, this original regime is occupied only by members of Caenolestidae and Didelphidae. A shift towards increased dietary specialization occurred at the origin of Australidelphia. The optimum specialization score for this regime is consistent with a reduction to two food types, with a bias towards one over the other. A similar regime shift occurred within Didelphidae, in the branch leading to *Thylamys*. Following this shift to increased dietary specialization in Australidelphia, there were three regime shifts to increased generalism in the branches leading to Petauridae, *Phalanger*, and Burramyidae. The regime occupied by members of Burramyidae has an optimum dietary specialization score of zero, indicating extreme dietary generalism. Shifts to an optimal diet consisting of a single food type occurred in the branch leading to *Phalanger gymnotis* and the branch leading to *Isoodon*.

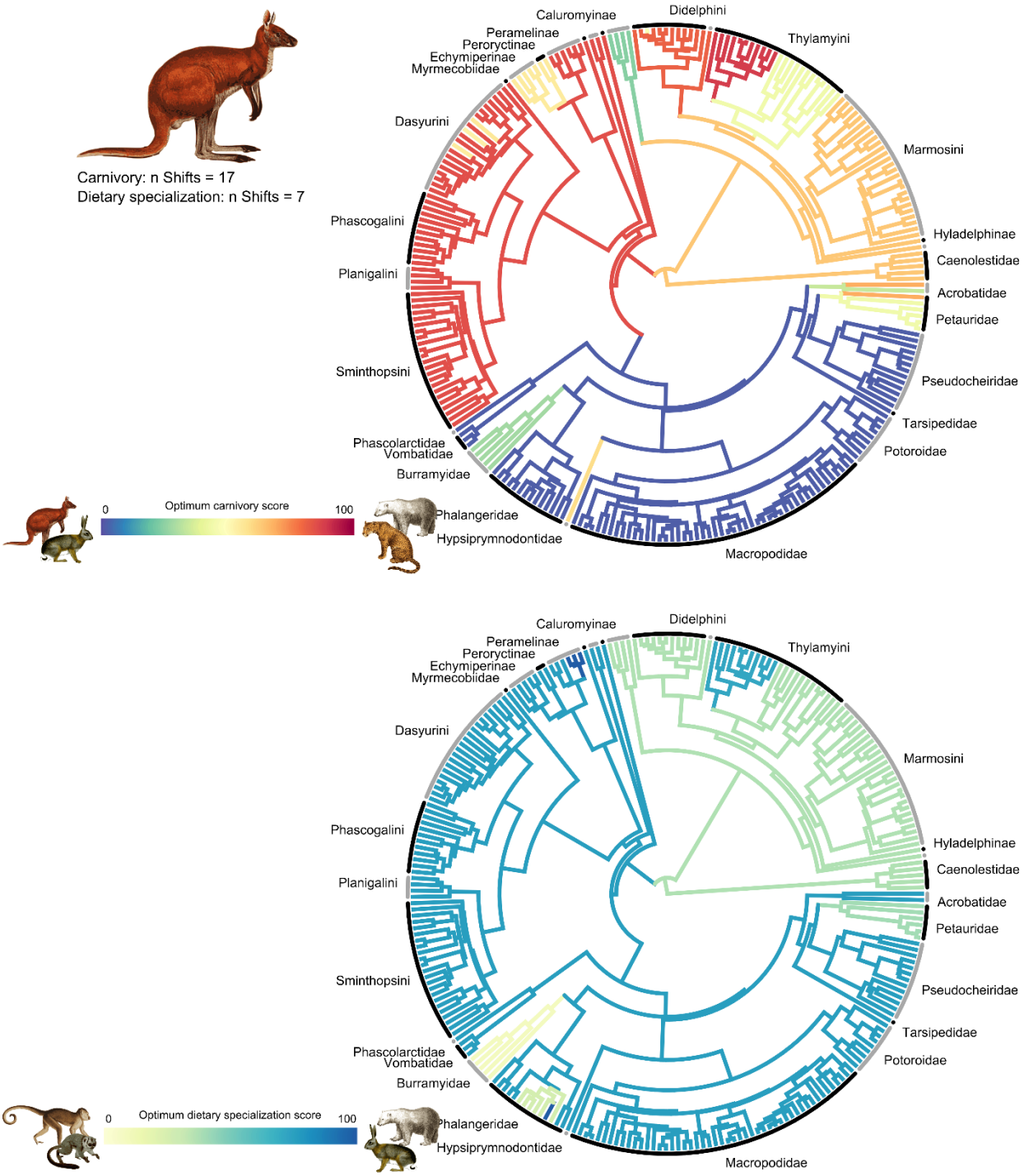
Discussion

The ancestral optimum diet of Marsupialia was shown in our study to be mesocarnivorous, with an early shift to increased vertivory at the origin of Australidelphia. In the current study, the ancestral optimum carnivory score is most similar to extant species whose most commonly consumed food type is invertebrates. This reinforces previous ancestral reconstructions of diet in Marsupialia that have reported an insectivorous ancestor, but contradicts their finding of unbroken maintenance of this insectivory through to contemporary members of Australidelphia (Amador and Giannini 2021). Additional discrepancies between the previous study and our findings exist, but these may be attributable to differences in methodology (ancestral diet reconstruction vs regime shift analysis of optimal dietary values) and diet scoring (categorical vs continuous).

A significant relationship between degree of carnivory and speciation rate was observed in Marsupialia. Hyperherbivores and hypercarnivores, and to some extent mesocarnivores, showed higher speciation rates than mesoherbivores and omnivores. Indeed, marsupial species that were scored as omnivorous using our carnivory variable are rare. Instead, carnivorous dasyurids and herbivorous diprotodontids comprise more of the marsupialian diversity. The radiation of these clades has been attributed to the aridification of Australia (Dodt *et al.* 2017; García-Navas *et al.* 2018), with later waves of diversification associated with the subsequent major expansion of grasslands (Kealy and Beck 2017; Celik *et al.* 2019). Thus, the diet-dependent speciation dynamic

observed in Marsupialia may have been reinforced or driven by the impact that historical environmental change had on specific clades within Marsupialia. More work would need to be done to delineate the contributions of diet and environment to marsupial diversification.

Evolutionary change in degree of carnivory and degree of dietary specialization was slow in both Marsupialia and Atlantogenata. Although diet still evolves under an OU process in these subclades, longer phylogenetic half-lives indicate that the centralizing tendency is weak, and the role of phylogenetic inertia is strong, suggesting an impediment to the evolution of a particular adaptation (Hansen and Orzack 2005). Unique reproductive, physiological, and geographical constraints have been posited as the cause of limited adaptability and diversification in marsupials (Sánchez-Villagra 2013). Phylogenetic niche conservatism and strong phylogenetic correlations have previously been reported within Marsupialia (Chemisquy *et al.* 2015; García-Navas and Rodríguez-Rey 2019).



522

523 **Figure S18.** Regime shifts in optimum carnivory score (top) and optimum dietary specialization
524 score (bottom) in Marsupialia. Branch color indicates the value of the optimum diet score. Position
525 of color changes represents the location of regime shifts. Images source: Wikimedia Commons.

Dietary regimes in Rodentia

Due to its large size, we separated Rodentia into four clades for regime shift analyses – Castorimorpha, Hystricomorpha, Sciuromorpha, and Myomorpha + Anomaluromorpha. At the origin of Castorimorpha, a hyperherbivorous diet with a small proportion of animal matter was optimal (Fig. S9). Multiple shifts in optimal degree of carnivory occurred within Castorimorpha, but the change in optimal carnivory score was small. All carnivory regimes in Castorimorpha show varying degrees of hyperherbivory. The dietary specialization regime occupied at the origin of Castorimorpha had an optimal specialization score indicative of a diet comprising equal proportions of two food types. This regime is still occupied by members of Hetermyinae. Independent shifts to complete dietary specialization as the optimum occurred in the branches leading to Castoridae and Geomyidae. A shift to an intermediate optimal specialization score indicative of a diet comprising three separate food types, both plant- and animal-based, occurred at the origin of Perognathinae. A shift to increased dietary generalism, with an optimal specialization score consistent with a diet comprising four different food types, occurred in the branch leading to Dipodomyinae.

Few shifts in optimum degree of carnivory or degree of dietary specialization occurred within Hystricomorpha (Fig. S10). Complete herbivory was optimum at the origin of Hystricomorpha. Two independent shifts to increased carnivory occurred. The regime shift at the origin of Dasyproctidae experienced only a slight increase in carnivory and maintained a hyperherbivorous optimum diet. In the branch leading to *Hoplomys gymnurus*, there was a shift to mesoherbivory. The optimum degree of dietary specialization represented a diet comprising equal proportions of two food types. Only one shift in degree of dietary specialization occurred – a shift to an optimum diet comprising three different food types in the branch leading to Dasyproctidae.

The original regime for degree of carnivory in Sciuromorpha had an omnivorous optimal diet (Fig. S11). Contemporary occupancy of this regime occurs only within Gliridae. Similar carnivory regimes arose in the branches leading to *Heliosciurus*, Glaucomyina, and *Tamiasciurus*. In the branch leading to Sciuridae and Aplodontiidae, there was a regime shift towards hyperherbivory. A similar regime arose in the branch leading to *Muscardinus* in Gliridae. Shifts to complete herbivory as the optimum occurred in branches leading to *Glis*, *Tamias*, *Marmota*, *Cynomys*, *Petinomys*, and *Glaucomys*. Regimes with mesoherbivory as the optimum diet arose in the branches leading to *Xerus* and *Callosciurus*. Omnivory arose as the optimum diet in the branches leading to *Graphiurus* and *Eliomys*. One shift to an optimum diet of mesocarnivory occurred in the branch leading to *Rhinosciurus*.

At the origin of Sciuromorpha, the optimum diet comprised four different food types, with a bias in favor of one food type over the others (Fig. S11). A similar regime arose in the branch leading tribe Callosciurini, minus *Lariscus* and *Exilisciurus*. Increases in dietary specialization to optimum diets comprising three different food types occurred in the branches leading to *Marmota*, Callosciurinae, and the branch leading to *Epixerus* and *Protoxerus*. Regimes with optimal specialization scores consistent with diets comprising two different food types occurred within *Sciurus* and in the branches leading to *Tamias*, *Myosciurus*, *Glis*, *Xerus rutilus*, and *Cynomys*. Complete specialization on a single food type arose as the optimum diet for regime shifts at the origin of Aplodontiidae and in the branches leading to *Eupetaurus* and *Rheithrosciurus*.

The optimum diet of the carnivory regime at the origin of Myomorpha + Anomaluromorpha was one of hyperherbivory (Fig. S12). This regime is still occupied by members of Anomaluromorpha, Dipodidae, Platacanthomyidae, Spalacidae, Neotominae, Tylomyinae, Nesomyidae, Murinae, and Calomyscidae. Similar hyperherbivorous regimes arose throughout Neotominae, Sigmodontinae, Murinae, and Gerbillinae, and a shift to complete herbivory occurred in the branch leading to Arvicolinae and Cricetinae. Regime shifts with more mesoherbivorous optimum diets occurred within Neotominae, Arvicolinae, Cricetinae, Nesomyidae, and Deomyinae, and throughout Murinae. Mesoherbivorous regimes also arose within Sigmodontinae, including a shift at its origin. Omnivory arose as the optimum diet within Neotominae, Sigmodontinae, Nesomyidae, and Gerbillinae, throughout Murinae, and in the branch leading to *Salpingotus* in Dipodidae. Shifts to mesocarnivory occurred in Sigmodontinae, Murinae, and the branch leading to *Allactaga* in Dipodidae. Hypercarnivory arose as the optimum diet within Neotominae, Sigmodontinae, Murinae, and at the origin of Deomyinae.

A diet consisting of two food types, one animal-based and one plant-based, was optimal at the origin of Myomorpha + Anomaluromorpha (Fig. S12). Contemporary members of this dietary specialization regime still exist in Anomaluromorpha and most subfamilies within Myomorpha. Regimes with shifts towards increased dietary generalism arose within Neotominae, Sigmodontinae, Arvicolinae, Cricetinae, Nesomyidae, and Murinae. Optimal degree of dietary specialization increased in regimes within Dipodidae, Neotominae, Sigmodontinae, Nesomyidae, Murinae, and Gerbillinae. Additional shifts to increased specialization occurred at the origins of Spalacidae and Lophiomyinae, as well as the branch leading to Arvicolinae and Cricetinae.

Discussion

It has been argued that the ancestral condition of Rodentia was omnivorous, and that their success as an order can be attributed to their dietary flexibility (Landry 1970). Based on the notion of an ancestral omnivorous condition, a shift away from omnivory and towards herbivory at the origin of Hystricomorpha has been suggested (Mess *et al.* 2008). Our results support an optimal herbivorous condition at the origin of Hystricomorpha, as well as at the origins of Castorimorpha and Myomorpha + Anomaluromorpha. Only Sciuromorpha showed an omnivorous optimum diet at its origin, with an early shift to a more herbivorous optimum in the branch leading to Aplodontiidae and Sciuridae. If the ancestral condition of Rodentia was omnivorous, our results indicate that there were multiple independent shifts towards increased herbivory that are associated with the origin of the rodent suborders. Due to limitations of our regime shift analyses resulting from phylogeny size and computational limits, the optimal dietary condition at the origin of crown Rodentia cannot be inferred from our results. However, extending the inference of our results suggests that the crown of Rodentia was herbivorous and not omnivorous.

Rodents represent the most speciose mammalian group, with some of the most specialized feeding apparatus within Mammalia (Cox *et al.* 2012; Gómez Cano *et al.* 2013), suggesting that diet has been important during their evolution. Despite this, diet was not found to be significantly associated with rodent diversification in the current study, or previously (Alhajeri and Steppan 2018). It was suggested by Alhajeri and Steppan (2018) that the opportunistic feeding behavior of most rodents, even those considered predominantly specialized for a given food type, renders diet classification of rodent species inaccurate. This opportunism therefore dilutes the signal of diet-dependent diversification.

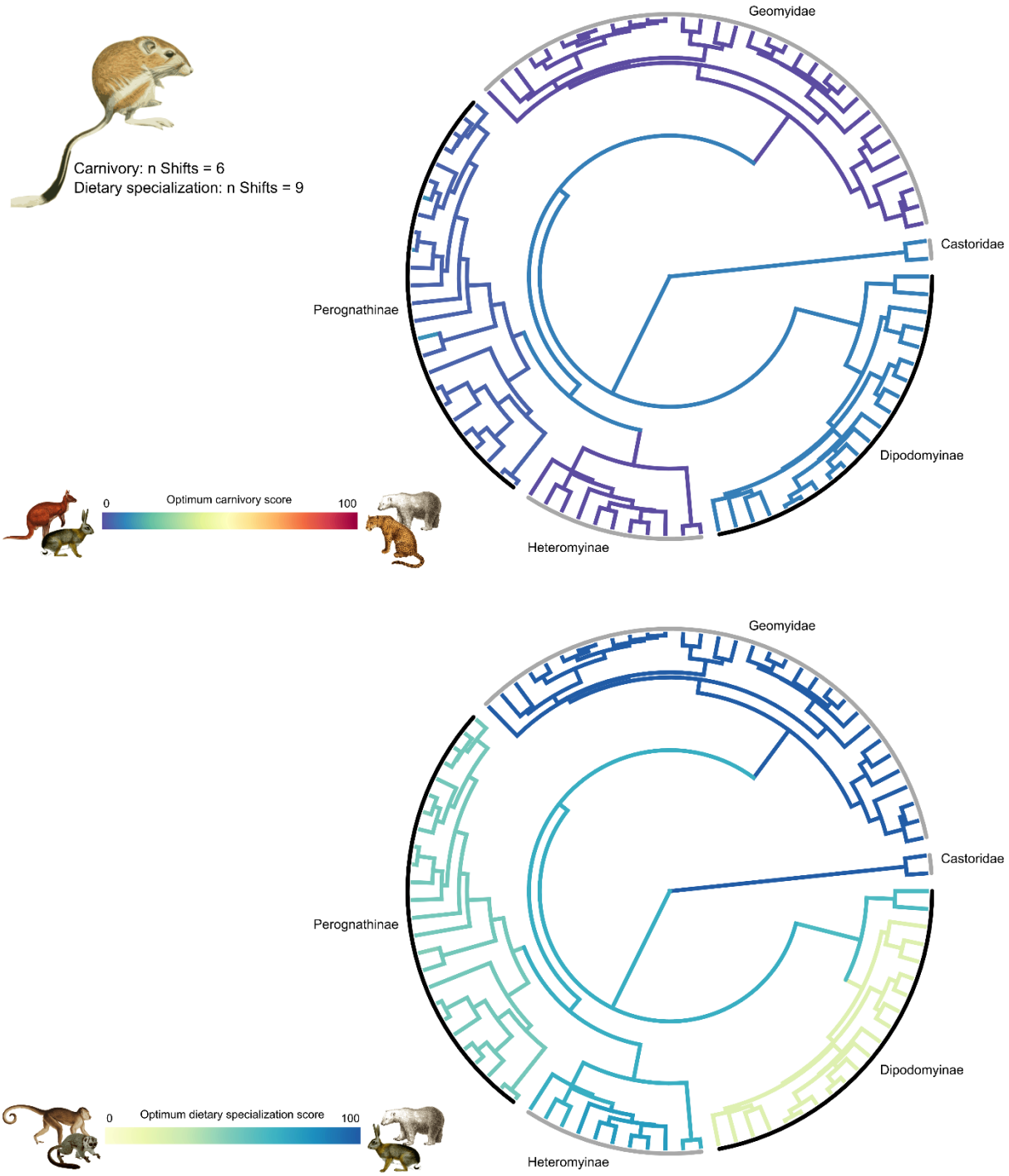


Figure S19. Regime shifts in optimum carnivory score (top) and optimum dietary specialization score (bottom) in Castorimorpha. Branch color indicates the value of the optimum diet score. Position of color changes represents the location of regime shifts. Images source: Wikimedia Commons.

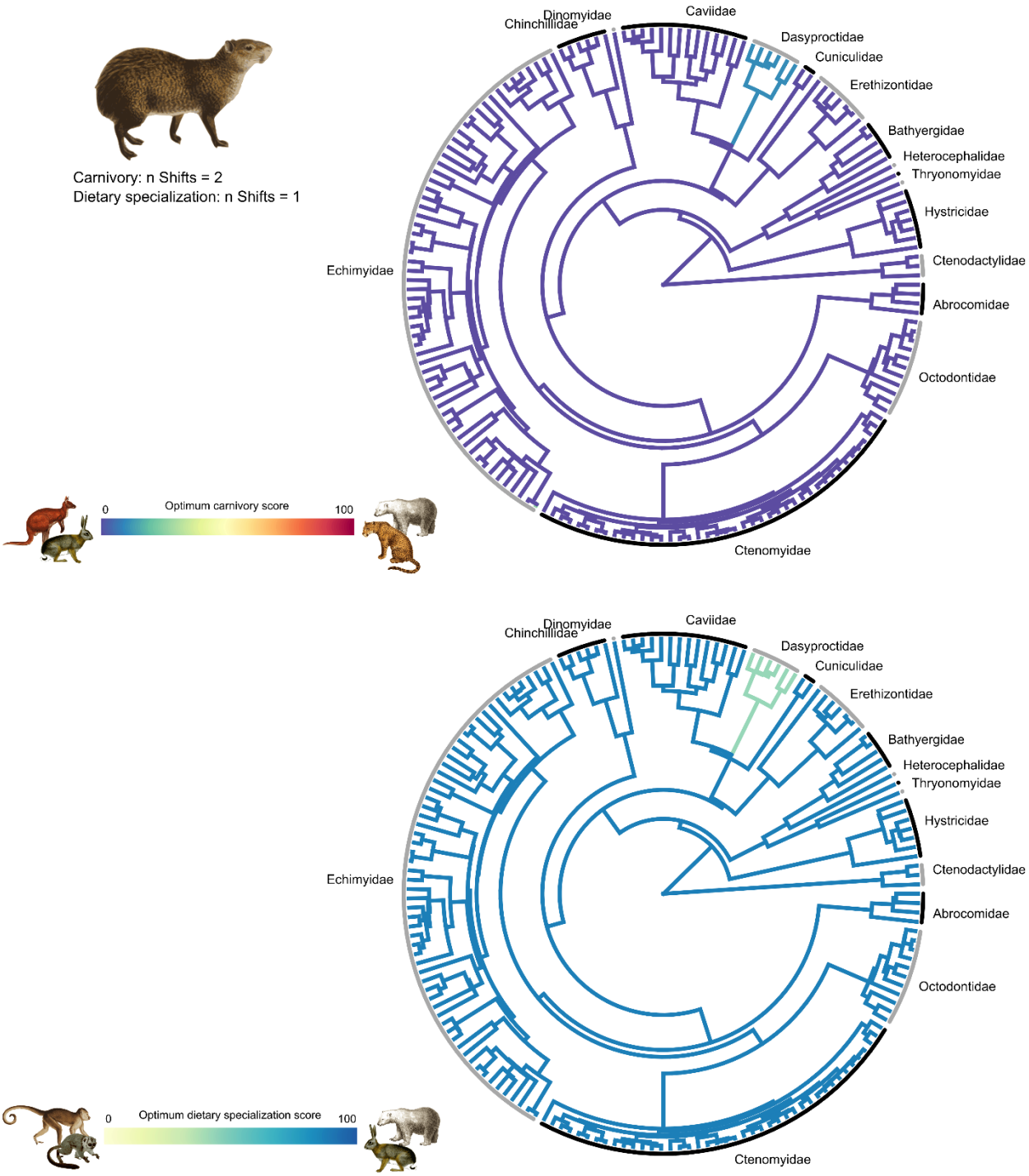


Figure S20. Regime shifts in optimum carnivory score (top) and optimum dietary specialization score (bottom) in Hystricomorpha. Branch color indicates the value of the optimum diet score. Position of color changes represents the location of regime shifts. Images source: Wikimedia Commons.

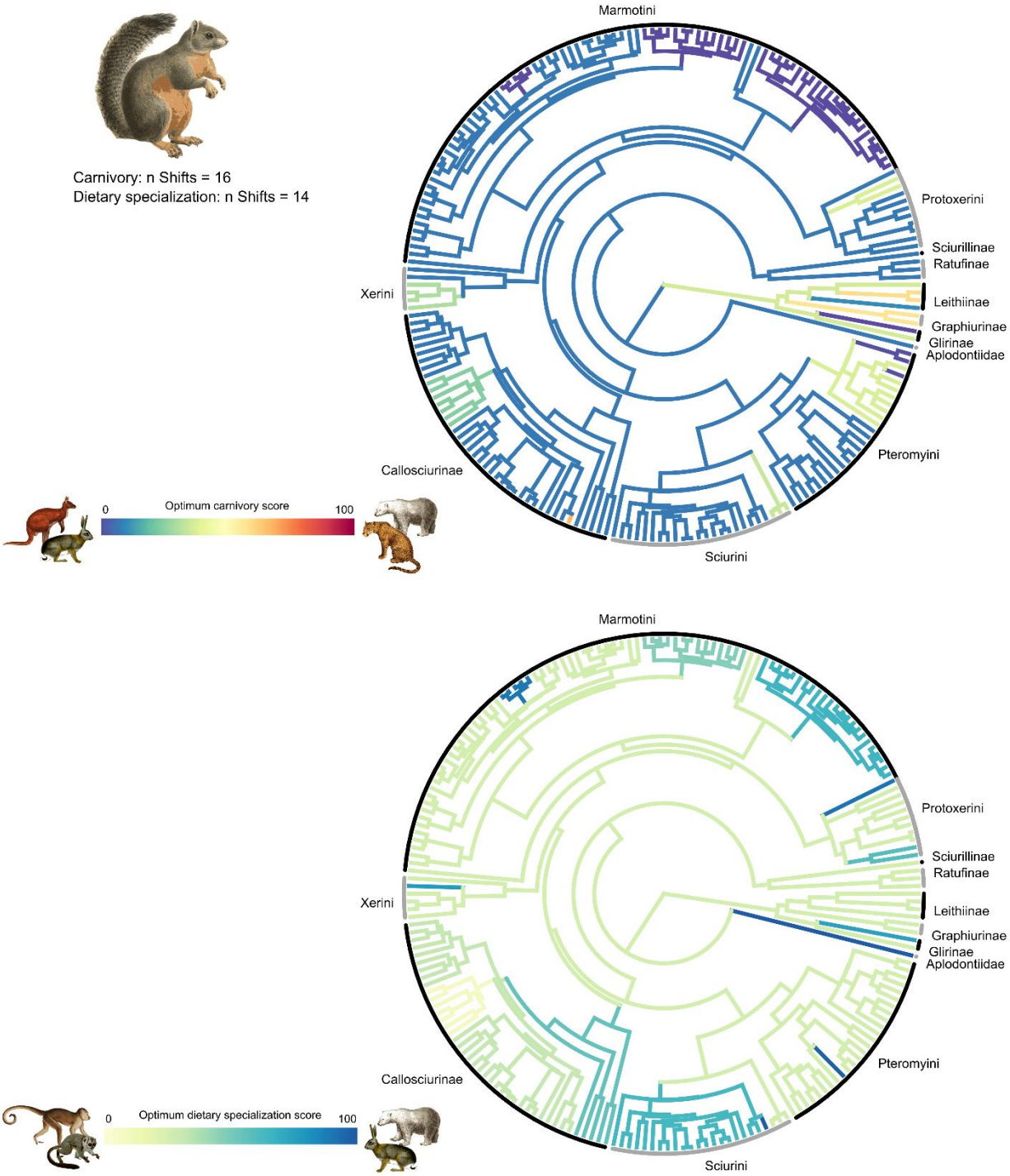


Figure S21. Regime shifts in optimum carnivory score (top) and optimum dietary specialization score (bottom) in Sciuromorpha. Branch color indicates the value of the optimum diet score. Position of color changes represents the location of regime shifts. Images source: Wikimedia Commons.

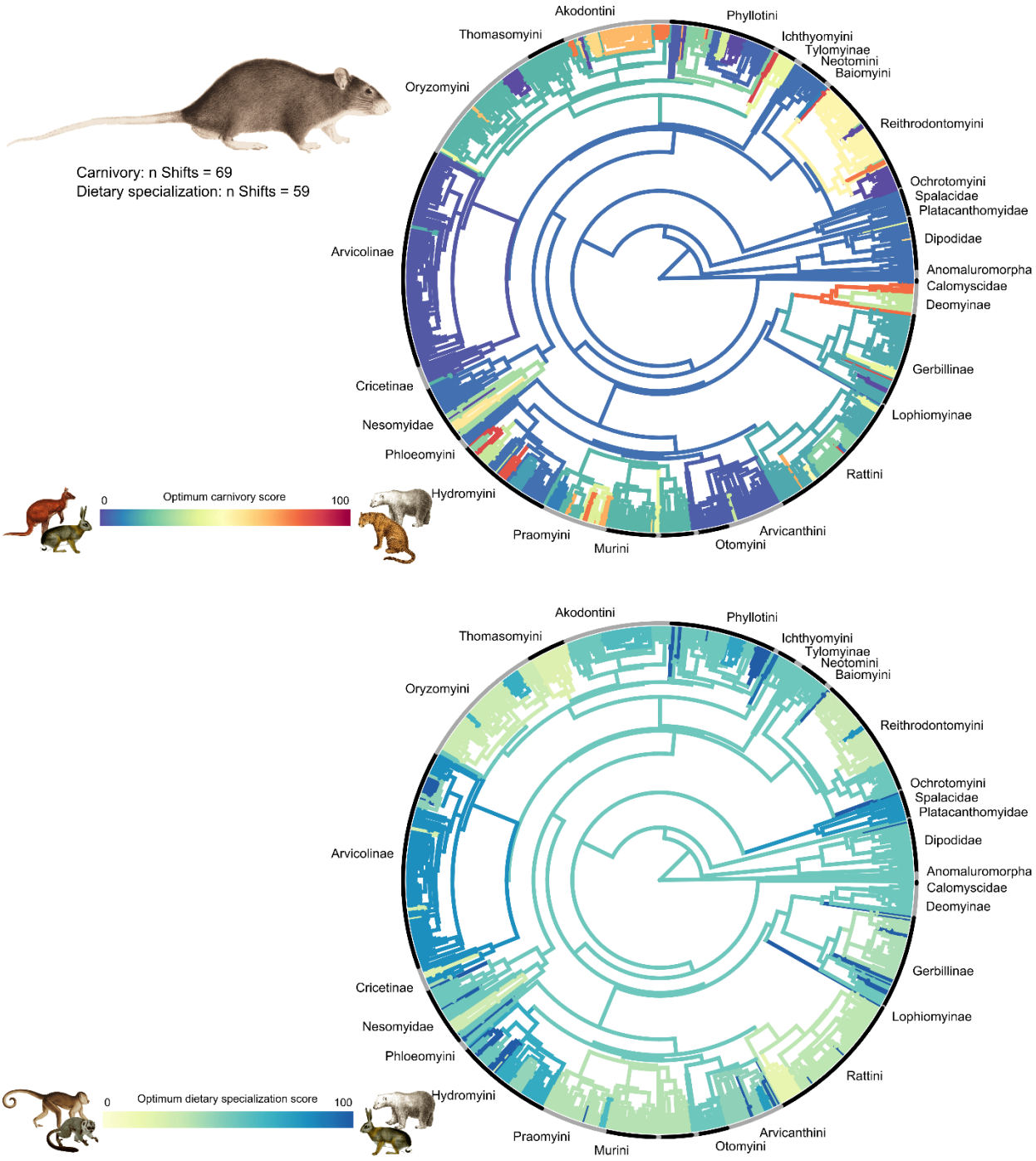


Figure S22. Regime shifts in optimum carnivory score (top) and optimum dietary specialization score (bottom) in Myomorpha + Anomaluromorpha. Branch color indicates the value of the optimum diet score. Position of color changes represents the location of regime shifts. Images source: Wikimedia Commons.

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