CHAPTER 1

The caviomorph rodents: distribution and ecological diversification

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1.1 The caviomorph radiation

The mammal fauna of the Neotropical Region can be divided into three distinct faunal strata reflecting younger and older faunal contingents (Simpson 1980; Webb & Marshall 1982). The first stratum is comprised of the ancient fauna of the early Cenozoic, which includes armadillos, giant anteaters, marsupials, and a diverse group of **autochthonous** ungulates. The second stratum is made up of allochthonous lineages, which includes hystricognath (caviomorph) rodents, primates, procyonids, cricetid rodents, emballonurid and vespertilionid bats, and trichechid sirenians. The third stratum includes other more recent taxa. Hystricognath rodents probably arrived from Africa between 45.4 and 36.7 Ma (Poux et al. 2006). The oldest known records of this South American endemic lineage are small (30–120g) caviomorph rodents, which occurred during the Middle Eocene in Peru (about 41 Ma; Antoine et al. 2012). Caviomorphs diversified rapidly into major clades during the Eocene-Oligocene (Antoine et al. 2012; Bertrand et al. 2012) and radiated in different directions, in terms of body size, ecomorphological, physiological, and behavioral traits. As a result, these animals exhibit ecological convergence with several orders of mammals such as hyracoids, ungulates, and lagomorphs (Eisenberg 1981; Mares & Ojeda 1982; Lessa et al. 2008). The rapid **adaptive radiation** and successful establishment of caviomorphs may have been due to colonization of a new region (South America) which was largely lacking competitors (ecological equivalents), with a diversity of food, habitat resources, and "empty" niches. As Patterson and Pascual (1972) noted, these proto-caviomorphs, found a vaccuum leading to rapid

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diversification in the early Oligocene, when "it is already possible to recognize all four caviomorph superfamilies" (p. 278).

The four superfamilies, Cavioidea, Chinchilloidea, Erethizontoidea, and Octodontoidea include 13 families, 56 genera and 246 extant species (Upham & Patterson 2012). The superfamily Cavioidea includes the Dasyproctidae (agouties), Cuniculidae (pacas), Caviidae (cavies and maras), and Hydrochoeridae (capybaras); the superfamily Erethizontoidea (New World porcupines) is monotypic with the Erethizontidae; Chinchilloidea includes the Chinchillidae (chinchillas, mountain and plains viscachas) and Dinomyidae; finally, the Octodontoidea includes the Abrocomidae, Octodontidae, Ctenomyidae, and Echimyidae (including Myocastoridae and Capromyidae) (Rowe et al. 2010; Upham & Patterson 2012; Pérez & Pol 2012). Within the Caviomorpha, the basal split consisted of the separation of the superfamilies Cavioidea + Erethizontoidea from Chinchilloidea + Octodontoidea, estimated at 37.9 Ma (middle to late Eocene). The Chinchilloidea/Octodontoidea divergence was inferred at 35.0 Ma (late Eocene), while the Cavioidea/Erethizontoidea separation occurred at the end of the Eocene (33.9 Ma) (Voloch et al. 2013).

Caviomorph rodents radiated and occupied a wide spectrum of landscapes, elevations, and habitats of the Neotropics, with one species, *Erethizon dorsatum*, ranging into the Neartic Region. Five families are mainly distributed thoughout the tropical region (Erethizontidae, Cuniculidae, Echymidae, Dinomyidae, and Dasyproctidae). The Myocastoridae, Ctenomyidae, and Chinchillidae are distributed in temperate regions, and Octodontidae and Abrocomidae are mostly distributed along the Andes. The family Caviidae exhibits the broadest distribution, covering most of South America. Overall, there are two major areas with the highest species density. One area includes the Amazonian biome, in the central-western region of tropical South America (between 0 and 10°S), and occupying the lowlands of western Brazil and the tropical Andean Forest of Ecuador and Peru. The other occurs within the Atlantic Forest along the eastern border of southern Brazil, (Upham & Patterson 2012; Ojeda et al. 2013; Ojeda et al. 2015).

Caviomorph rodents have diversified into an extraordinary variety of lifestyles and feeding niches, hereafter **macroniches** (*sensu* Eisenberg 1981; Chapter 2 in this book). A simplified illustrated version of some representatives of this functional diversity is shown in Fig. 1.1. Recent analyses on hypothetical ancestral areas and ecological states of major clades of caviomorphs and their diversification in new "**adaptive zones**" during their evolution in South America have suggested the Amazonia region as the ancestral area in the diversification of proto-caviomorphs, and that they were most likely associated with **saxicolous** modes of life and a diet based on grasses, leaves and fruits (Ojeda et al. 2015).

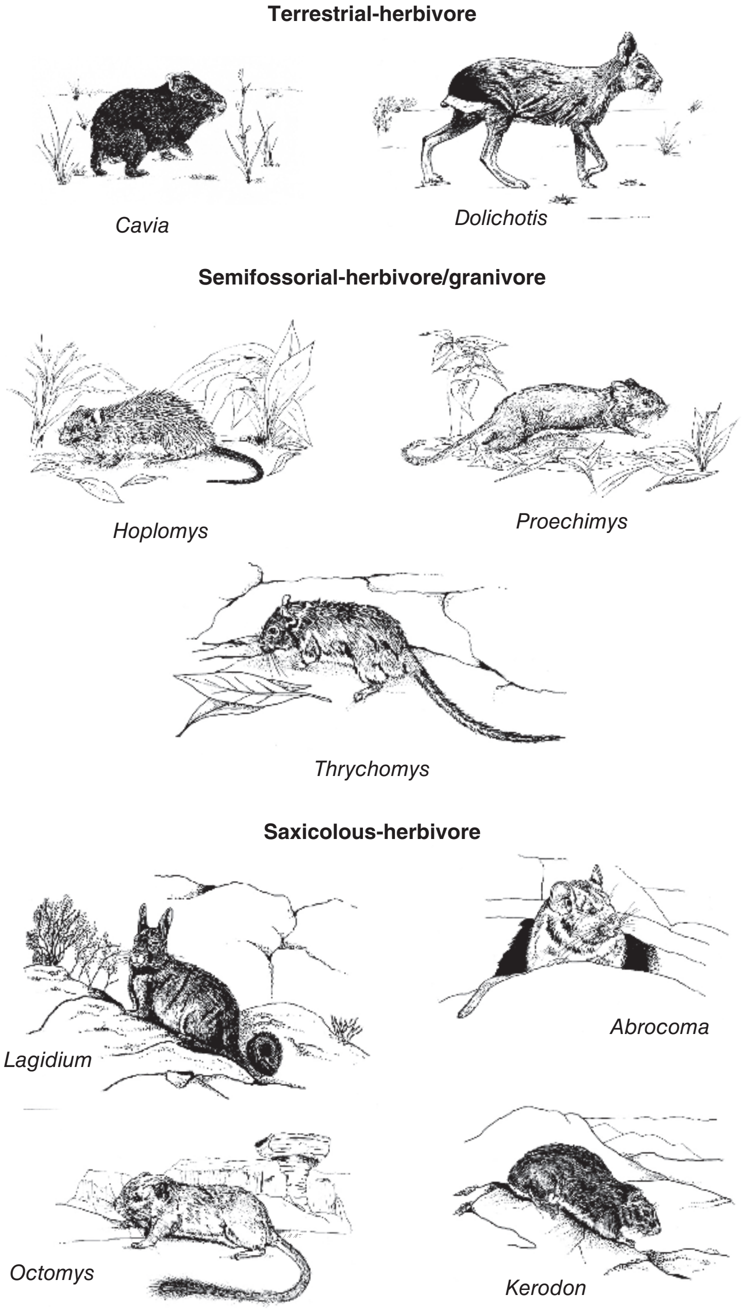


Figure 1.1 Representative genera of major caviomorph macroniches combining modes of life, such as substrate use, and feeding habits. Original drawings by Benjamín Bender.

Subterranean-herbivore

Ctenomys

Spalacopus

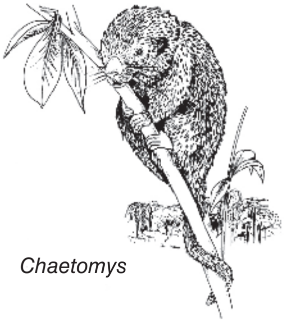
Fossorial-herbivore

Lagostomus

Tympanoctomys

Microcavia

Arboreal-herbivore



Chaetomys

Cuscomys

Figure 1.1 (*continued*)

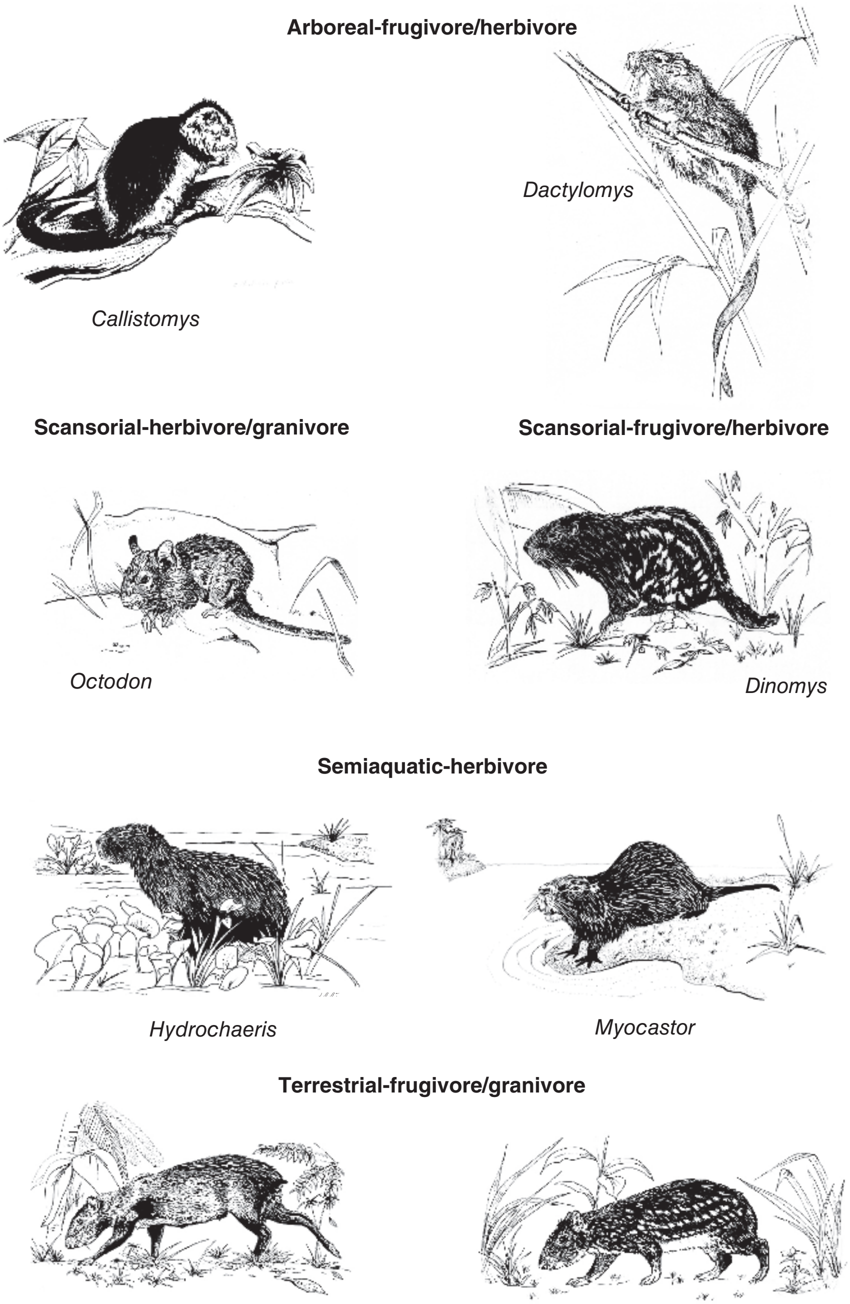


Figure 1.1 (*continued*)

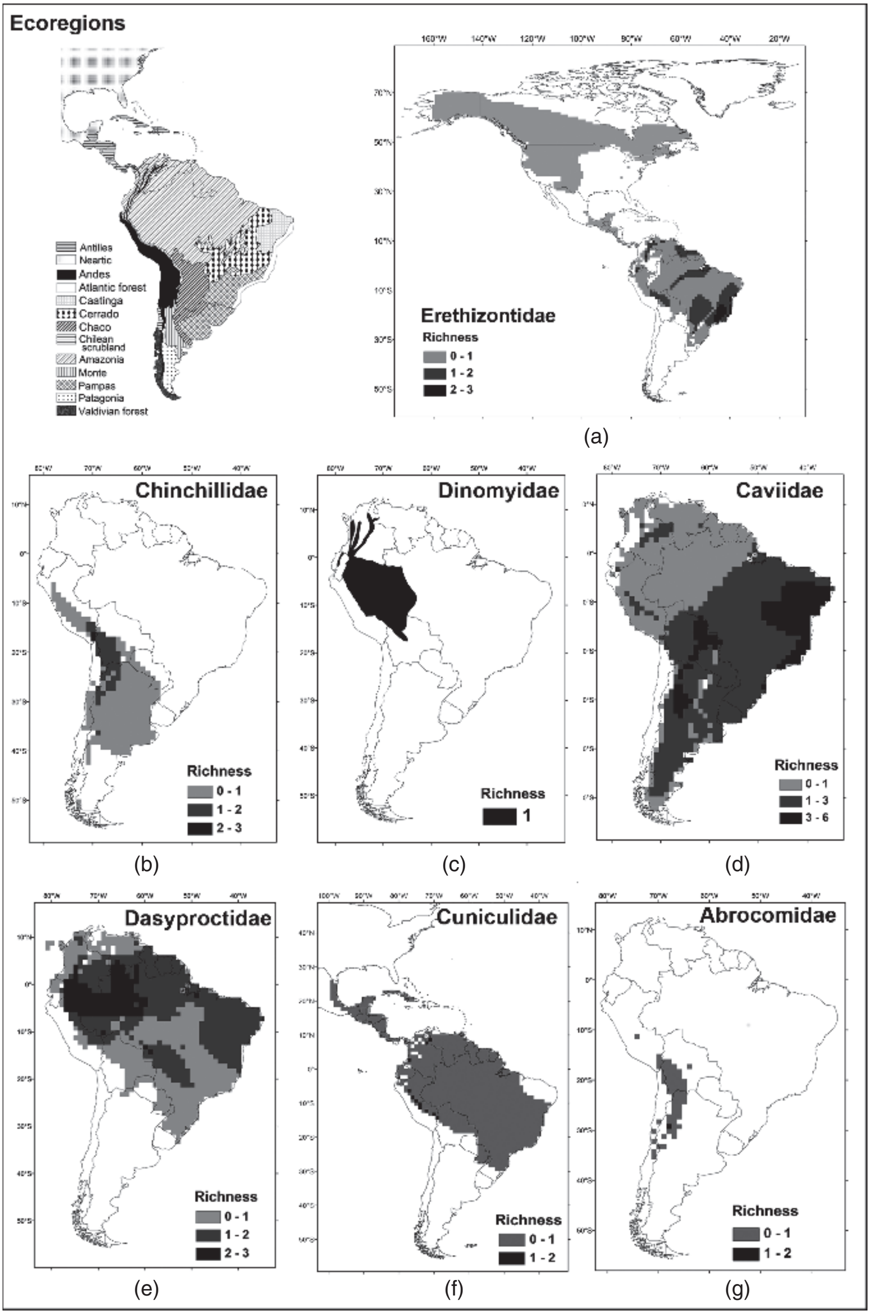
1.2 The families

1.2.1 Erethizontidae

- *Diversification and taxonomic relationships*. Erethizontidae (New World porcupines) includes 7% and 6% of caviomorph genera and species respectively, with one genus distributed in North America (*Erethizon*). The family is comprised of 15 species belonging to at least three genera (*Coendou*, *Erethizon*, *Chaetomys*) (Voss 2011). The genus *Sphiggurus* is a synonym of *Coendou*, although other authors recognize *Sphiggurus* and *Echinoprocta* as distinct genera from the spiny *Coendou* (Bonvicino et al. 2002; Woods & Kilpatrick 2005). The Superfamilies Erethizontoidea and Cavioidea split in the early Oligocene and are strongly supported as sister groups (Upham & Patterson 2012; Fabre et al. 2013).
- *Distribution*. The family Erethizontidae is distributed from the Arctic of North America to northern Mexico and east to the Appalachian mountains, and from southern Mexico through Ecuador and northern Argentina as its southernmost range (Fig. 1.2a). Only the genus *Erethizon* inhabits forests and wooded regions of the Neartic Region. Species density in South America is highest at the eastern margins of the continent, mainly in the Atlantic forest and Cerrado ecoregions, and decreases towards northern and southern geographic ranges (Fig. 1.2a). Historical biogeographical analyses suggest the Amazonia ecoregion as the most likely ancestral area of the Superfamilies Erethizontoidea and Cavioidea (Upham & Patterson 2012; Ojeda et al. 2015).
- *Niche use*. Reconstructions of ancestral state macroniches suggest that New World porcupines evolved from an arboreal form with a diet based on fruits and leaves (Ojeda et al. 2015). The extant genera are arboreal (*Chaetomys*, *Coendou*, *Sphiggurus*) and scansorial (*Echinoprocta*, *Erethizon*) with herbivorous and frugivorous diets and a body mass ranging from 1,300 to 14,000 g (Table 1.1).
- *Sociality*. New World porcupines have been classified as solitary (*Coendou*), and solitary and colonial (*Erethizon*).

1.2.2 Chinchillidae

- *Diversification and taxonomic relationships*. The family Chinchillidae (Chinchillas, mountain viscachas, and plains viscachas) is composed of three genera, *Chinchilla*, *Lagidium*, and *Lagostomus* and seven species (Woods & Kilpatrick 2005). Chinchillidae and Dinomyidae (*Dinomys*) are strongly considered a monophyletic group forming the superfamily Chinchilloidea (Huchon & Douzery 2001; Spotorno et al. 2004; Poux et al. 2006; Huchon et al. 2007; Rowe et al. 2010; Upham & Patterson 2012).
- *Distribution*. Species of Chinchillidae are distributed along the central and southern Andes and throughout most of Patagonia in southern South America, extending latitudinally from 5–40° S (Fig. 1.2b). Most species of *Chinchilla*



(a)

(b) (c) (d)

(e) (f) (g)

Figure 1.2 Geographic distribution of caviomorph families and species density.

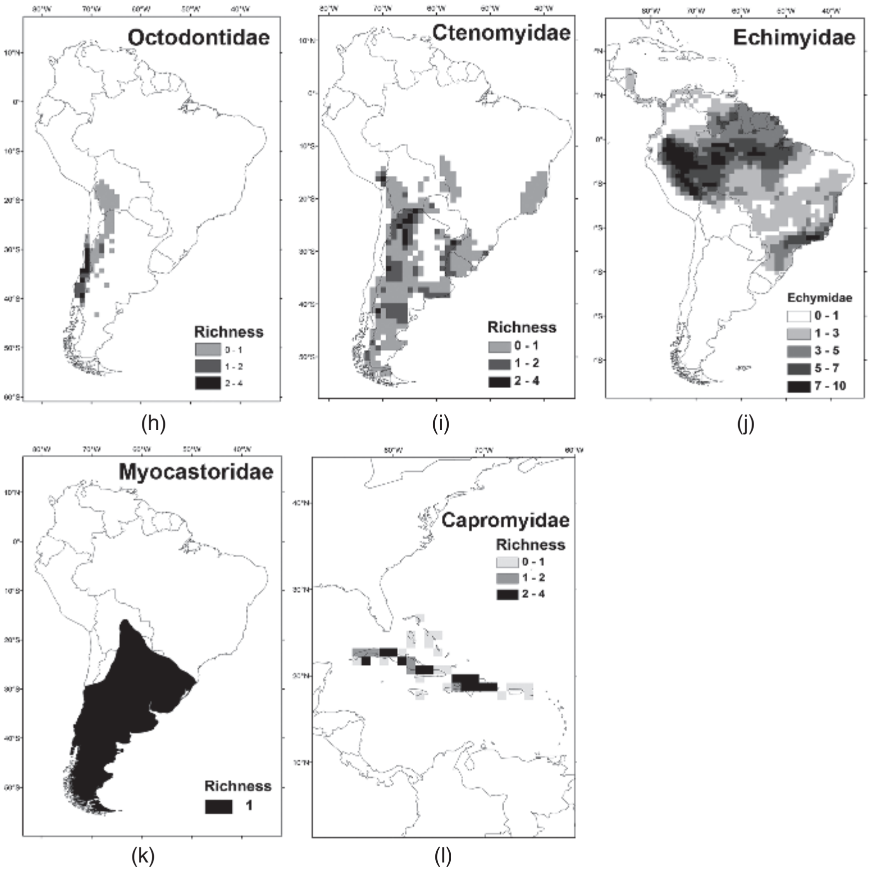


Figure 1.2 (*continued*)

and *Lagidium* are restricted to the arid landscapes of the Andes (Altiplano and Puna) and Patagonia, inhabiting rocky surfaces and among boulders. However, the plains viscacha, *Lagostomus maximus*, occurs in the Pampas, the Monte desert, and the Chacoan thorn scrub. The highest density of species is located in the arid Andes of Peru and Bolivia (Fig. 1.2b).

- *Niche use*. Reconstructions of ancestral state macroniches suggest that Chinchillidae evolved from an herbivorous, saxicollous ancestor. Some species retained this condition whereas others (e.g. *Lagostomus maximus*) evolved a fossorial mode of life. The body size of chinchillids ranges between 390 g and 8840 g. Suggested pairs of ecological equivalents are: *Lagostomus*, *Cynomys*, *Chinchilla*, *Otospermophilus*, *Sciurotamias*, *Lagidium* (see Mares & Ojeda 1982).
- *Sociality*. Chinchillas, mountain viscachas, and plains viscachas live in social groups of up to several hundred individuals (Table 1.1; Chapter 2 in this book).

Table 1.1 Ecoregions (see Fig. 1.2), macroniches, body mass (g), and general social behavior of caviomorph genera.

Taxon	Ecoregions	Macroniches	Body mass	Social behavior
Erethizontidae				
Chaetomys	Atlantic Rainforest	Arboreal-herbivore	1300	
Coendou	Atlantic Rainforest, Amazonia	Arboreal-frugivore, herbivore	4000–5000	Solitary
Echinoprocta	Amazonia	Scansorial-frugivore	831	
Erethizon	Tundra grasslands, forests, desert scrublands	Scansorial-herbivore	5000–14000	Social; solitary
Sphiggurus	Atlantic Rainforest	Arboreal-herbivore	1150–1340	
Chinchillidae				
Chinchilla	Andes	Saxicolous-herbivore	390–500	Social; multi-family groups
Lagidium	Patagonia	Saxicolous-herbivore	750–2100	Social; family groups
Lagostomus	Pampas, Monte Chaco	Semifossorial-herbivore	3520–8840	Social; family groups
Dinomyidae				
Dinomys	Amazonia	Scansorial-frugivore, herbivore	10000–15000	Pair living or small groups; rich repertoire of vocalizations; intricate calls
Caviidae				
Cavia	Amazonia, Chaco, Cerrado	Terrestrial-herbivore	550–760	Low levels of sociality, hierarchical promiscuity
Galea	Amazonia, Chaco, Caatinga, Cerrado, Patagonia, Pampas	Terrestrial-herbivore	150–550	Low levels of sociality, hierarchical promiscuity
Microcavia	Monte, Chaco, Patagonia	Semifossorial-herbivore	250–326	Low levels of sociality, hierarchical promiscuity
Dolichotis	Monte, Chaco, Patagonia	Terrestrial (cursorial)-herbivore	1000–2700 9000–16000	Pair living or small groups; (D. salinicola); monogamous (D. patagonum)
Hydrochoerus	Amazonia, Caatinga, Cerrado, Atlantic Rainforest, Chaco	Semiaquatic-herbivore	35000–65000	Social; harem defense polygony
Kerodon	Caatinga, Cerrado	Saxicolous-herbivore	750–1080	Social; resource defense polygyny

(*continued overleaf*)

Table 1.1 (*continued*)

Taxon	Ecoregions	Macroniches	Body mass	Social behavior
Dasyproctidae				
Dasyprocta	Amazonia, Atlantic Rainforest Pantanal	Terrestrial-frugivore, herbivore	1430–8500	Pair living or small groups (1–7 individuals)
Myoprocta	Amazonia	Terrestrial-frugivore, herbivore	800–1450	Pair living; family groups
Cuniculidae	Amazonia, Chaco, Cerrado	Terrestrial-frugivore, herbivore	9200–9500	Pair living; female parental care; male and females live in different burrows
Cuniculus				
Ctenomyidae				
Ctenomys	Cerrado, Caatinga Chaco, Pampas, Patagonia, Monte, Amazonia (Yungas)	Subterranean-herbivore	92–900	Mostly solitary, some social
Octodontidae				
Aconaemys	Andean-Valdivian Forest	Fossorial-herbivore, granivore	83–170	Some social
Octodon	Chilean scrublands	Scansorial-herbivore, granivore	92.5–260	Mostly social
Octodontomys	Monte	Scansorial-herbivore	158	Social
Octomys	Monte	Saxicolous-herbivore	95–120	Solitary
Pipanacoctomys	Monte	Fossorial-herbivore	90–128	Solitary (pers. obs.)
Salinoctomys	Monte, Chaco	Fossorial-herbivore	88–110	Social
Spalacopus	Matorral, Andean	Subterranean-herbivore	80–120	Solitary (pers. obs.)
Tympanoctomys	Monte, Patagonia	Fossorial-herbivore	82–91	
Abrocomidae				
Abrocoma	Monte-Chilean scrublands	Saxicolous-herbivore	157.3–307	Social; small (3–4) family groups
Cuscomys	Andes	Arboreal-herbivore	910	
Echimyidae				
Dactylomys	Amazonia	Arboreal-frugivore, herbivore	650–750	
Kannabateomys	Atlantic Rainforest	Arboreal-folivore-herbivore	380–460	Pair living; monogamy; biparental care

Olallamys	Amazonia	Arboreal-folivore-herbivore		
Callistomys	Atlantic forest	Arboreal-frugivore-herbivore	267–480	
Diplomys	Amazonia	Arboreal-frugivore-herbivore	227	
Echimys	Amazonia, Atlantic Rainforest	Arboreal-frugivore-herbivore	220–900	Solitary, social, or pair living
Isothrix	Amazonia	Arboreal-frugivore-herbivore	400–450	
Makalata	Amazonia	Arboreal-frugivore-herbivore	249–395	
Phyllomys	Atlantic Rainforest	Arboreal-frugivore-herbivore	145–325	
Carterodon	Cerrado	Semifossorial-frugivore-herbivore	158	
Clyomys	Cerrado, Pantanal	Fossorial-herbivore	100–270	Social
Euryzygomatomys	Cerrado, Atlantic forest	Fossorial-frugivore-herbivore	170–200	
Hoplomys	Amazonia	Terrestrial-frugivore,granivore	450	
Lonchothrix	Amazonia	Arboreal-frugivore-herbivore	190	
Mesomys	Amazonia	Arboreal-frugivore-herbivore	150–220	
Proechimys	Amazonia	Terrestrial-frugivore, granivore	104–360	Solitary
Thrichomys	Caatinga, Cerrado	Scansorial-frugivore, granivore	115–450	
Trinomys	Caatinga, Cerrado, Atlantic forest	Terrestrial-frugivore, granivore	150–280	
Myocastoridae				
Myocastor	Chaco, Pampas, Patagonia, Monte, Valdivian Forest, Chilean Scrubland, Amazonia	Semiaquatic-herbivore	3500–5800	Social; hierarchical promiscuity
Capromyidae				
Capromys	Antilles	Arboreal-frugivore	3061–6900	Solitary; pair living, small family groups
Geocapromys	Antilles	Scansorial-folivore-frugivore	660	Social; family groups
Mesocapromys	Antilles	Scansorial-frugivore	483–1217	
Mysatele	Antilles	Scansorial-folivore-frugivore	1799	Social
Plagiodontia	Antilles	Scansorial-folivore-frugivore	1267	Small family groups
Heptaxodontidae	Antilles			Extinct

Notes: Detailed information about caviomorph social systems can be found in Maher and Burger (Chapter 2 in this book).

1.2.3 Dinomyidae

- *Diversification and taxonomic relationships*. This family belongs to the group of the giant, long-headed rodents which were quite diverse in the Late Miocene (Rinderknecht et al. 2011). The extant representative belongs to a monotypic genus known as pacarana, *Dinomys branickii*. Based on recent molecular analyses, *Dinomys* is strongly allied with members of the Chinchillidae (Huchon & Douzery 2001; Spotorno et al. 2004; Poux et al. 2006; Huchon et al. 2007; Rowe et al. 2010; Upham & Patterson 2012) and constitutes a monophyletic Chinchilloidea superfamily, with *Lagostomus* occasionally considered as sister species to *Dinomys* (Upham & Patterson 2012).
- *Distribution*. The pacarana has a latitudinal geographic range from about 10° S to 18° S, through the tropical forest of western Amazonia and the Andean foothills of Venezuela, Colombia, Ecuador, and Peru to the Bolivian Yungas (Fig. 1.2c). The fossil distribution of the family was broader, with specimens known from Argentina, Colombia, Venezuela, and Uruguay (Rinderknecht et al. 2011).
- *Niche use*. The natural history of the pacarana is practically unknown, and most behavioral repertoire has been recorded from captive animals (White & Alberico 1992). Eisenberg and Redford (1999) suggested that pacaranas are nocturnal, eat a diet of fruits, leaves and herbs, and are climbers (Table 1.1).
- *Sociality*. Pacaranas live in social groups of up to five individuals (White & Alberico 1992, and references therein). Pacaranas display an elaborate communication system, with foot stomping, teeth chattering and different vocalizations (Collins & Eisenberg 1972; Eisenberg 1974).

1.2.4 Caviidae

- *Diversification and taxonomic relationships*. The caviids are a diverse clade divided into three widely divergent extant lineages: Caviinae (cavies), Dolichotinae (maras), and Hydrochoerinae (capybaras). These three major lineages are well differentiated from a morphological and ecological perspective (Pérez & Pol 2012). The family is comprised of six genera (*Cavia*, *Galea*, *Microcavia*, *Dolichotis*, *Hydrochoerus*, and *Kerodon)* and 18 species (Woods & Kilpatrick 2005). Their main diversification occurred during the middle to late Miocene and they became morphologically and taxonomically diverse in the late Miocene (Pérez & Pol 2012). The available fossil record suggests that the initial split of Caviidae into three major lineages may have occurred around 11.8–13.5 Ma and that three modern and morphologically distinct lineages of Caviidae (Hydrochoerinae, Dolichotinae, and Caviinae) were already present and diverse about 6.1–9.07 Ma (Pérez & Pol 2012).
- *Distribution*. Caviids are distributed across the South American continent and their habitats include almost all major South American biomes, from moist savannas to thorn forests and desert scrublands. The highest species density occurs in the dry south-central Andes in the Cerrado and Caatinga ecoregions (Fig. 1.2d).

- *Niche use*. The ancestral proto-caviid is hypothesized to have been terrestrial with a diet of grasses and leaves (Ojeda et al. 2015). Their macroniche radiation was primarily in the modes of locomotion, with terrestrial (*Dolichotis*), semiaquatic (*Hydrochoerus*), semifossorial (*Microcavia*), and saxicolous (*Kerodon*) species. However, this characterization for some genera should be taken cautiously (as with other groups); for example, *Kerodon* could be classified as scansorial-saxicolous due to strong association with rock outcroppings, similar to other saxicolous desert rodents (e.g. hyraxes of eastern Africa; Mares & Lacher 1987). The ecological equivalents of some caviids are *Dolichotis salinicola*: cottontail rabbit, *D. patagonum*: jackrabbit, and the small cavies, *Microcavia*, *Galea*, and *Cavia*, with ground squirrels (Mares & Ojeda 1982).
- *Sociality*. The caviids show a broad social repertoire ranging from solitary (*Galea*, *Cavia*) and pair-living (*Dolichotis*), to colonial (*Microcavia*), and highly social (*Kerodon*, *Hydrochoerus*). There is much literature and thorough reviews on general behavior repertoires, and comparative social and mating systems for most of the caviids (Lacher 1981; Taber 1987; Honeycutt et al. 2007; MacDonald et al. 2007; Wolff & Sherman 2007; Chapters 2 and 10 in this book).

1.2.5 Dasyproctidae

- *Diversification and taxonomic relationships*. The family Dasyproctidae (agoutis and acouchis) contains two genera (*Dasyprocta* and *Myoprocta*) and 13 species. The family includes several extinct genera from the Oligocene to middle Miocene that inhabited Argentina, Bolivia, and Colombia (McKenna & Bell 1997). Dasyproctids have been placed in the superfamily Cavioidea by Woods (1982) and McKenna and Bell (1997). Dasyproctidae split from Caviidae and Cuniculidae in the early Oligocene (Wyss et al. 1993; Hartenberger 1998). A recent molecular analysis suggests that Caviidae and Dasyproctidae are sister groups (Upham & Patterson 2012).
- *Distribution*. Both genera have a tropical distribution and inhabit mainly subtropical and tropical rainforests. Family distribution extends from northern South America to 30° S. The highest species density is found in the northwestern portion of South America, with a decrease in richness towards the south (Fig. 1.2e). *Dasyprocta* also is found in the Chaco and Cerrado ecoregions (Emmons & Feer 1997).
- *Niche use*. Both genera are terrestrial, diurnal, and mainly herbivores with a diet consisting of fruits, succulent plants, leaves, seeds and roots (Emmons 1990; Grzimek 1990). Reconstructions of the ancestral state macroniche suggest that dasyproctids evolved from a terrestrial form with a diet based on grasses, fruits and leaves (Ojeda et al. 2015).
- *Sociality*. Agoutis and acouchis display different types of behavior (solitary, pair-living and family groups) (Table 1.1).

1.2.6 Cuniculidae

- *Diversification and taxonomic relationships*. The family Cuniculidae contains two species, commonly referred to as pacas, placed in the single genus *Cuniculus* (*C. paca* and *C. taczanowskii*) (Nowak 1991; Wilson & Reeder 2005). The familial status of this taxon has long been a matter of debate (McKenna & Bell 1997). Currently, Cuniculidae is considered the proper familial name and C*uniculus* the genus within this family. Chromosomal (George & Weir 1974), allozyme (Woods 1982), and DNA sequence (Rowe & Honeycutt 2002; Upham & Patterson 2012) characters support the recognition of Cuniculidae as a distinct family contained by the superfamily Cavioidea (Woods 1982; McKenna & Bell 1997; Upham & Patterson 2012). Within the superfamily Cavioidea, the Cuniculidae and Caviidae diverged in the early Miocene, about 22.6 Ma (Voloch et al. 2013).
- *Distribution*. The geographic distribution of these animals extends from east-central Mexico to southeast Paraguay and northeast Argentina (Nowak 1991; Botello et al. 2005; Myers et al. 2006). Species density is highest at the tropical Andes region (Fig. 1.2f). *Cuniculus paca* has a broad range from southern Mexico to northern Argentina, including Central America. Elevationally, *C. paca* is found from sea level to 1600 m.a.s.l. (Pérez 1992). *C. taczanowskii* is found in mountains of Peru, Ecuador, Colombia, and northwest Venezuela (Woods & Kilpatrick 2005), at elevations of 2000–3500 m.a.s.l.
- *Niche use*. Pacas are primarily terrestrial herbivores, nocturnal, and consume foliage, roots, nuts, seeds, and fruits (Nowak 1991). Reconstructions of ancestral state macroniches suggest that Cuniculidae evolved from a terrestrial form with a diet based on grass-leaves. This ancestral condition is shared with Caviidae (Ojeda et al. 2015). *Cuniculus* exhibits ecological convergence with chevrotains (genus *Tragulus*), and rabbits (Mares & Ojeda 1982; Feldhammer et al. 1999).
- *Sociality*. Pacas live solitarily or in male-female pairs (Nowak 1991; Pérez 1992).

1.2.7 Abrocomidae

- *Diversification and taxonomic relationships*. The family is comprised of two genera, *Abrocoma* (with eight species) and *Cuscomys* (recently discovered, with one extant and one extinct species) (Woods & Kilpatrick 2005). The existing members of Abrocomidae and fossil taxa date to the late Miocene (McKenna & Bell 1997; Vucetich et al. 1999). Abrocomidae was formerly treated as a subfamily of either Echimyidae (Ellerman 1941) or Octodontidae (Pascual 1967), but now is regarded as a distinct family and the most basal lineage within the superfamily Octodontoidea (Upham & Patterson 2012).
- *Distribution*. The family Abrocomidae (chinchilla rats) is distributed in the central and southern Andes in Peru, Bolivia, Argentina, and Chile. Most species are known only from the vicinity of the type locality (Glanz & Anderson 1990; Woods & Kilpatrick 2005) and are described based on single records

(Braun & Mares 2002). *Abrocoma cinerea* and *A. benetti* exhibit relatively large distributions (14–31° S and 27–35° S, respectively). In general, species ranges do not overlap (Fig. 1.2g) except for *A. cinerea*, which potentially coexists with *A. budini* (Catamarca and La Rioja provinces, Argentina) and with *A. famatina* (in La Rioja province) (Woods & Kilpatrick 2005). Different types of habitats occur along this range, with mainly rocky areas within Mediterranean scrub habitat, grasslands and cloud forests that go from sea level (in Chile) up to 5000 m.a.s.l. (Braun & Mares 2002; Woods & Kilpatrick 2005).

- *Niche use*. The genus *Abrocoma* is specialized in rocky habitats (e.g. saxicollous), whereas *Cuscomys* (*C. ashaninka*) is arboreal. Both genera have an herbivorous diet based on grasses and leaves (Taraborelli et al. 2011; Ojeda et al. 2015).
- *Sociality*. The genus *Abrocoma* is social, living in small family groups (Taraborelli et al. 2011).

1.2.8 Octodontidae

- *Diversification and taxonomic relationships*. Octodontids are a monophyletic group composed of eight genera and 14 species with restricted geographic distributions. The monophyly of the group is based on morphological and molecular characters (Nedbal et al. 1994; Köhler et al. 2000; Gallardo & Kirsch 2001; Honeycutt et al. 2003). However, there is some ambiguity over the monophyly and branching relationships among some genera of octodontoids (e.g. *Spalacopus* and *Aconaemys*) (Honeycutt et al. 2003; Upham & Patterson 2012). The origin of the family dates back to the late Miocene, between 7.79 to 9 Ma (Opazo 2005; Rowe et al. 2010; Upham & Patterson 2012), with its major diversification occurring during the Plio-Pleistocene.
- *Distribution*. The family Octodontidae is distributed along both sides of the Andes in Argentina, Bolivia, and Chile, between 15° and 40° S. Species density is highest in the Andean and Chilean scrubland ecoregions, mainly in central Chile (Fig. 1.2h). The family occurs in a wide range of habitats (Table 1.1), from coast, rainforests and Mediterranean habitats to the Andean region and desert scrublands (Reig 1981; Mares & Ojeda 1982; Gallardo et al. 2007).
- *Niche use*. Historical biogeographical analysis suggests that the arid lands of the Monte desert are the ancestral area of the family (Ojeda et al. 2013; Ojeda et al. 2015) with saxicolous, terrestrial, and semifossorial modes of life, and a diet of grasses and leaves. During its evolution, octodontids split it into two well-differentiated clades, expanded their geographic range, dispersed to other ecoregions, and diversified into different macroniches (Ojeda et al. 2013). One clade is restricted to Argentina and is comprised by one saxicolous (*Octomys*) and one semifossorial xeric-adapted (*Tympanoctomys, Pipanacoctomys*) species. Both species of this clade are solitary and inhabit arid lands (the Monte desert). The other clade is restricted to Chile and includes the subterranean and social genus *Spalacopus*, the semifossorial *Aconaemys*, and the terrestrial generalist and generally social *Octodon*, distributed in the

Mediterranean sclerophyllous woodlands and semiarid open scrublands of central Chile. This clade is the sister group of the scansorial and similarly social genus *Octodontomys*, which is found in pre-Andean Monte and Puna habitats of northwestern Argentina, southern Bolivia, and northeastern Chile (Rivera et al. 2014). Mares and Ojeda (1982) have suggested several ecological equivalents of octodontid rodents (e.g. *Octomys*—*Neotoma*; *Octodon*—ground squirrels; *Spalacopus*—pocket gophers; *Aconaemys*—*Microtus*). *Tympanoctomys barrerae* exhibits ecological convergence with *Dipodomys microps* (Dipodomyidae) in North America, and *Psammomys obesus* (Gerbillidae) in northern Africa and Israel (Mares et al. 1997; Ojeda et al. 1999).

- *Sociality*. Octodontids are mostly social (Rivera et al. 2014) with some solitary genera (*Octomys*, *Tympanoctomys*, and *Pipanacoctomys*).

1.2.9 Ctenomyidae

- *Diversification and taxonomic relationships*. The family Ctenomyidae, along with Echimyidae, is one of the most diverse families of South American hystricognath rodents. Ctenomyidae is a monophyletic lineage and sister taxa to Octodontidae (Lessa & Cook 1998; Honeycutt et al. 2003; Rowe et al. 2010; Upham & Patterson 2012). The family is comprised of a single genus, *Ctenomys*, which is characterized by high species richness with approximately 60 recognized species (Woods & Kilpatrick 2005). Tuco-tucos have the largest chromosomal variation within mammals, with diploid numbers ranging from $2n = 10$ to $2n = 70$ (Novello & Lessa 1986; Cook et al. 1990), but they are quite uniform in morphology, suggesting an explosive radiation (Reig 1989; Lessa & Cook 1998; Castillo et al. 2005) since its appearance in the late Pliocene (Reguero et al. 2007; Verzi et al. 2010). Ctenomyid and Octodontid species appear to have diverged in the early Pliocene (Upham & Patterson 2012).
- *Distribution*. Ctenomyids (tuco-tucos) are distributed from southern Peru and southern Brazil to Tierra del Fuego through parts of Chile and most of Argentina, Bolivia, Paraguay, and Uruguay (Reig et al. 1990). The family is found in a wide range of habitats from the Andean Puna above 4000 m.a.s.l. to the coastal dunes of the Atlantic, and from the mesic and humid Pampas to the dry Chaco and Monte desert. Several species show restricted distributional ranges and some are known only from the type locality. Species density is highest in northwestern Argentina (Fig. 1.2i).
- *Niche use*. *Ctenomys* species are subterranean and, spend less than 1% of total time outside their burrows (Lessa et al. 2008). Tuco-tucos are herbivorous and preferentially feed on roots, herbs and stems. Along with Abrocomidae and Octodontidae, they share an ancestral herbivorous feeding niche of grasses and leaves (Ojeda et al. 2015).
- *Sociality*. Tucos-tucos are generally solitary, with the exception of *C. sociabilis* and a few other species (see Table 7.1 in Chapter 7 in this book) which are social (Lacey & Wieczorek 2003).

1.2.10 Echimyidae

- *Diversification and taxonomic relationships*. Echimyidae (spiny rat) is the most diverse family of caviomorph rodents, including 22 genera and about 91 species (Upham et al. 2013; Table 1.1). Fabre et al. (2013) have suggested an early Miocene radiation (between 23–16 Ma) of the extant echimyid genera connected to allopatric speciation and ecologically driven diversification.
- *Distribution*. Spiny rats are distributed through most of the tropical lowlands, from Honduras to northern Argentina, between latitudes 10° N and 30° S. Higher species density is found in the northwestern (Amazonian and Yungas forests) and southeastern (Atlantic forest) portions of its distribution (Fig. 1.2j). These rodents occupy a wide range of habitats from the Amazonian and Atlantic forest, to the semiarid Caatinga, Cerrado thorn scrub, and Pantanal biomes. The body mass of these rodents ranges between 100 and 900 g.
- *Niche use*. The family represents a good example of evolutionary radiation with high species diversity (Fabre et al. 2013). Within Echimyidae, three monophyletic groups are present: one group comprised of the Myocastoridae (with the semiaquatic *Myocastor*) and three terrestrial echimyid genera *Thrichomys*, *Proechimys*, and *Hoplomys*. A second group is comprised of an arboreal echimyid clade (genus *Dactylomys*, *Kannabateomys*, *Isothrix*, *Echimys*, *Makalata*, *Phyllomys*, *Mesomys*, and *Lonchothrix*), and a third group is comprised of the Capromyidae (hutias) and the three echimyid genera *Trinomys*, *Clyomys*, and *Euryzygomatomys* (Fabre et al. 2013). Based on the arboreal spiny rats found in the Amazonian (e.g. *Echimys*, *Dactilomys*) and eastern Brazilian Atlantic forest (*Phyllomys*, *Kannabateomys*), Leite and Patton (2002) have suggested that the common ancestors of tree rats and bamboo rats lived in a continuous forest during the warmer periods about 5 Ma. During the cooler periods around 3.8 Ma this "continuous forest" contracted, resulting in the vicariance of the Amazonian and Atlantic forests. Several other studies have also found a connection between Amazonian and Atlantic forests (Costa 2003).

  The radiation and macroniche diversification of spiny rats are associated with arboreal and terrestrial modes of life and the frugivorous habits. The exceptions are *Trinomys yonenagae* which shows a trend towards fossoriality (Santos & Lacey 2011) and the genera *Clyomys* and *Euryzygomatomys*, which shows adaptations to fossorial life (Table 1.1). The most recent common ancestor of spiny rats is inferred to be a ground-dwelling taxon that subsequently diverged into fossorial, semiaquatic, and arboreal habitats. The colonization of the arboreal niche constituted the keystone event of the echimyid radiation (Fabre et al. 2013; Ojeda et al. 2015). The hypothetical ancestor of the arboreal forms of Echimyidae is thought to have occupied a feeding niche of fruits and leaves, whereas terrestrial spiny rats have an ambiguous ancestral feeding niche of grass leaves and fruits seeds (also shared with the Myocastoridae and Capromyidae; Ojeda et al. 2015).

- *Sociality*. Very little is known of the social behavior of spiny rats; however, some species are solitary whereas others are monogamous and colonial (Silva et al. 2008; Table 1.1; also see Chapter 2 in this book and Table 7.1, Chapter 7 in this book).

1.2.11 Myocastoridae

- *Diversification and taxonomic relationships*. The family is composed of a single species, the nutria or coypu, *Myocastor coypus*. Myocastorids presumably evolved in the Oligocene in South America from an echimyid of the subfamily Adelophomyinae (Woods et al. 1992.) and diversified during the Miocene (Upham & Patterson 2012). Patterson and Pascual (1972) and Patterson and Wood (1982) treated myocastorids as a subfamily of Echimyidae, based on morphological similarities; this hypothesis has been supported by molecular data (Huchon & Douzery 2001; Galewski et al. 2005), which related *Myocastor* with various echimyids traditionally referred to as Eumysopinae. Recent molecular analyses of this Myocastoridae–Echimyidae relationship (Upham & Patterson 2012) recommend that Myocastoridae be treated as a synonym of Echimyidae.
- *Distribution*. Coypus are present in Brazil, Bolivia, Chile, Paraguay, Argentina, and Uruguay (Fig. 1.2k). Throughout distribution it is associated with mesic habitats, swamps, lakes, rivers, and streams with nearby woodlands (Woods et al. 1992).
- *Niche use*. *Myocastor coypus* is a semiaquatic species inhabiting areas near bodies of water (Bertolino et al. 2005). Historical biogeographical analyses of the family suggest an ambiguous ancestral biome (shared with a group of Echimyidae) comprised of Amazonia and the Catinga-Cerrado- Chaco areas. A reconstruction of the Myocastoridae ancestral state macroniche is ambiguous, suggesting a semifossorial-terrestrial-semiaquatic form with a diet based on grasses, leaves, fruits and seeds (Ojeda et al. 2015). Coypus are similar in their overall body form and mode of life to the North American muskrat, *Ondatra zibethicus* (Mares & Ojeda 1982).
- *Sociality*. The coypu lives in family groups composed of a dominant male, several females, other adult males, and juveniles (Guichón et al. 2003).

1.2.12 Capromyidae

- *Diversification and taxonomic relationships*. The family Capromyidae is composed of eight genera and about 20 species, of which around half of the species are extinct and most of the living species are endangered. These rodents resemble the coypus (*Myocastor*) and have sometimes been placed in that family. Capromyids have been treated as a subfamily of Echimyidae, based on morphological characters (Patterson & Pascual 1972; Patterson & Wood 1982). Molecular evidence support this synonymy including a well-supported sister relationship between *Capromys* and *Myocastor* within the Echimyidae

(Huchon & Douzery 2001; Leite & Patton 2002; Galewski et al. 2005). Recent molecular phylogenetic analyses find support for a monophyletic Echimyidae group that includes *Capromys* and *Myocastor*, and place capromyids at the base of Echimyidae (Upham & Patterson 2012; Fabre et al. 2013; Upham et al. 2013).

- *Distribution*. The family Capromyidae (West Indian hutias) is found in the Caribbean islands, reaching its greatest diversity in Cuba (Woods & Kilpatrick 2005; Borroto-Paez & Mancina 2011; Fig. 1.2.l).
- *Niche use*. The natural history of most of the species of this family is poorly known and anecdotal with the exception of *Capromys* (Borroto-Paez & Mancina 2011). Most hutias are terrestrial (*Capromys*), but some are scansorial (*Geocapromys*, *Plagiodontia*, *Mysateles*). They are primarily herbivorous feeding mainly on leaves and fruits, but also incorporate small vertebrates leading to a more omnivorous diet (Table 1.1).
- *Sociality*. Hutias nest in trees or rock crevices and are social, living in groups of about two or more individuals (Phillips et al. 1991).

1.3 General social behavior

A major aim of this book is to highlight the diversity of caviomorph rodent social behavior. We offer a brief overview of the general trends in terms of sociality that have evolved in different clades (Table 1.1; Fig. 1.3). Maher and Burger (Chapter 2 in this book) provide a detailed discussion of inter- and intraspecific patterns in social systems. Caviomorphs display a broad range of social structures, with about 75% of their families including one or more social species (Kleiman 1974; Lacey & Sherman 2007). Most family members in the four major lineages (i.e. superfamilies) exhibit solitary and social behavioral repertoires, whereas families whose behaviors are almost entirely social are Abrocomidae, Myocastoridae, Capromyidae, Dinomyidae and Chinchillidae (Fig. 1.3). A recent analysis by Sobrero et al. (2014) suggests the ancestrality of social behavioral attributes in hystricognath rodents.

We support the assertion made by several authors that caviomorph rodents are excellent models for studying the evolution of sociality and causes of variation in social systems within and between taxa (Hayes et al. 2011; Maher & Burger 2011). However, we would also emphasize the need to understand behavior as a cause and not just a consequence of evolution (Duckworth 2009). In this respect, a phylogeny, coupled with morphological, ecological, and physiological attributes of caviomorphs, will provide an excellent ground to explore the role of behavior as a causal factor of evolutionary change.

As Duckworth (2009) has pointed out, the interconnection of behavior and environmental changes highlight “the need to understand the sources of behavioral change in order to evaluate the relative importance of behavioral and environmental changes in driving or inhibiting evolution.” In our case, the

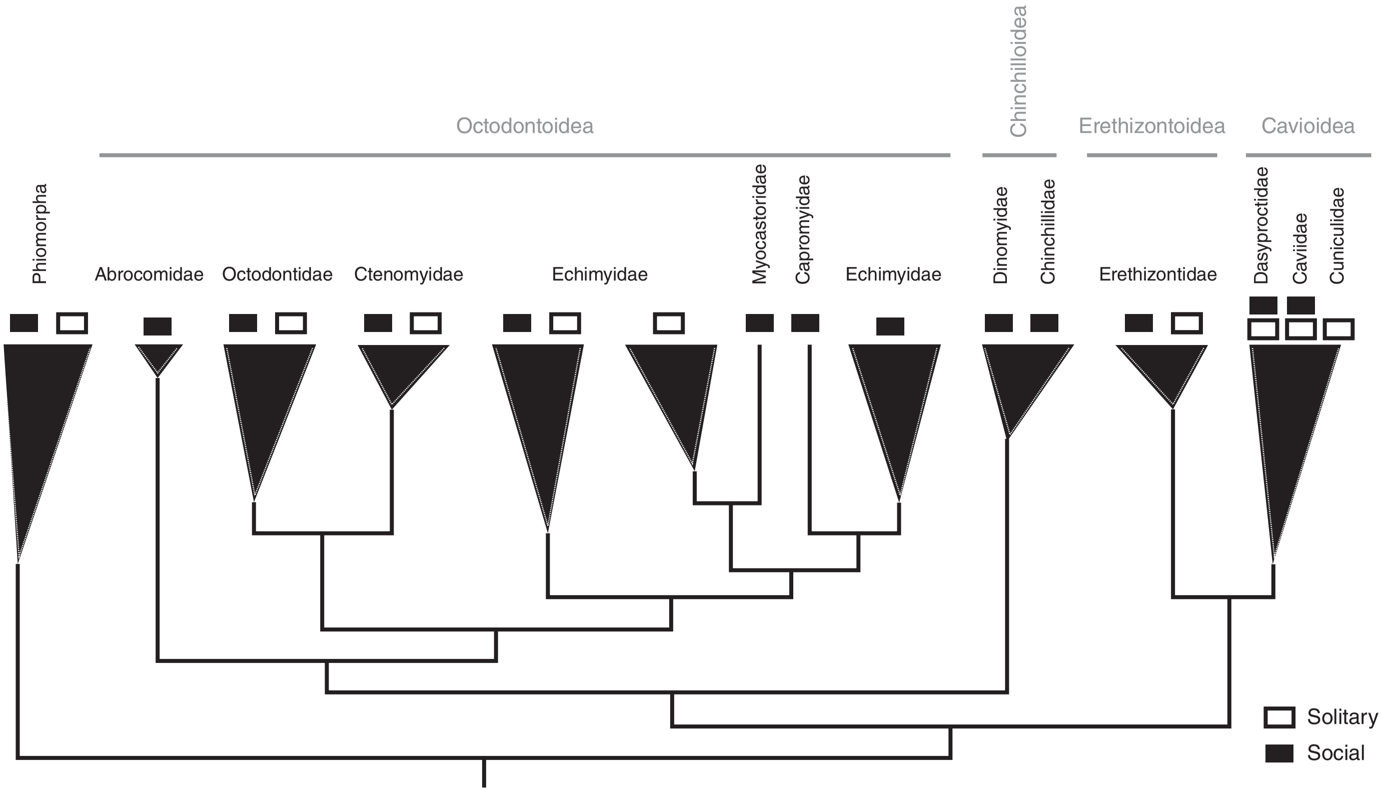


Figure 1.3 Illustrative graphic which summarizes the general behavior (solitary and social) in major caviomorph lineages (superfamilies and families). Phylogeny after Upham & Patterson (2012).

roles played by behavioral shift (i.e. novel behavior), and behavioral plasticity (i.e. adaptation) in conjunction with environmental changes, are necessary for an understanding of the radiation of caviomorph rodents.

1.4 Synthesis and future directions

Caviomorph rodents are one of the oldest and most conspicuous lineages of the South American biota. They are found from the Artic of North America to the tip of the southern cone of South America, over a wide spectrum of topographic reliefs, elevations and habitats, reaching their highest species densities within the hotspots of the tropical Andes, Amazonia and Atlantic forests. The hystricognath rodents colonized South America about 43 Ma and rapidly diversified into major clades, with an extraordinary diversity in body sizes, ecology, physiology, and behavioral attributes. Concomitant with this, their ecological radiation and speciation (e.g. 246 species) in South America filled approximately 16 macroniches; in contrast, their African relatives (Phiomorpha) total about 35 species and only fill a few macroniches, mainly associated with terrestrial, saxicolous, fossorial, and subterranean modes of life and have a narrow dietary spectrum of grasses, roots, tubercles, crops, and fallen fruits.

The aim of this chapter was to emphasize the integration of geographical distribution and ecological radiation within a phylogenetic framework (Losos 1996; Wiens & Donoghue 2004; Ricklefs 2007; Upham et al. 2013), offering a solid blueprint for exploring the evolutionary trends and diversity of social behavior in caviomorphs, as well as the evolutionary role of behavior (Duckworth 2009). This integrative approach offers an opportunity to explore the ecological radiation, niche plasticity, and behavioral repertoire of caviomorphs, where habitats, carrying capacity, demography, and feeding adaptations are among the determining factors of social structure (Eisenberg 1981). Recent contributions offer examples of phylogenetic, biogeographic, and ecological integrative research of different caviomorph lineages (Honeycutt et al. 2007; Upham & Patterson 2012; Ojeda et al. 2013; Fabre et al. 2013; Upham et al. 2013; Ojeda et al. 2015). Within a sound phylogenetic framework, the rich array of caviomorph ecology, habitat, diet and modes of life can provide the basis for a more comprehensive understanding of the evolution of caviomorph social behavior (Rowe & Honeycutt 2002; Honeycutt et al. 2007; Lacey & Ebensperger 2007; Lacey & Sherman 2007; Macdonald et al. 2007; Duckworth 2009).

As we are able to integrate intrinsic attributes and different factors (e.g. morphology, physiology, ecology, distribution, resource dispersion, among others) with a better understanding of behavioral repertoire, we envision that caviomorphs will be good test models for unresolved issues in evolutionary biology. In particular, there is a need to integrate geographical distribution and ecological radiation within a proper phylogenetic framework (Losos 1996; Wiens & Donoghue 2004; Ricklefs 2007; Upham et al. 2013). The phylogenetic approach allows us to disentangle whether or not the evolution of ecological or behavioral traits is the result of common ancestry or a response to similar environmental pressures (i.e. convergence). An example of this phylogenetic approach has been applied in caviid rodents in order to test for the evolution of complex social behavior (Rowe & Honeycutt 2002). Recent phylogenetic reconstructions to determine transitions in sociality and mating systems in mammals support the evolution of cooperative breeding from strict monogamous lineages (Lukas & Clutton-Brock 2013).

Finally, the challenge for future studies in behavior is to ascertain how the different types of behaviors have their impact on the rate of evolutionary diversification (Duckworth 2009). The integrative approach offers the opportunity to explore ecological radiation, niche plasticity, and patterns of species assembly at the regional pool and community level, and also provides a fertile matrix for disentangling the evolutionary trends of the rich behavioral repertoire of major caviomorph lineages.

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