SOCIOBIOLOGY OF CAVIOMORPH RODENTS
AN INTEGRATIVE APPROACH

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WILEY Blackwell
Sociobiology of Caviomorph Rodents
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An Integrative Approach

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To Marcela and Erika
Contents

Acknowledgments, ix
Notes on contributors, xi
Introduction, xv

1 The caviomorph rodents: distribution and ecological diversification, 1
   Ricardo A. Ojeda, Agustina A. Ojeda & Agustina Novillo

2 Diversity of social behavior in caviomorph rodents, 28
   Christine R. Maher & Joseph R. Burger

3 Comparative neurobiology and genetics of mammalian social behavior, 59
   Annaliese Beery, Yasmin Kamal, Raúl Sobrero & Loren D. Hayes

4 Developmental underpinnings of social behavior, 91
   Valentina Colonnello, Ruth C. Newberry & Jaak Panksepp

5 Dispersal in caviomorph rodents, 119
   Eileen A. Lacey

6 Mechanisms of social communication in caviomorph rodents, 147
   Gabriel Francescoli, Selene Nogueira & Cristian Schleich

7 Causes and evolution of group-living, 173
   Luis A. Ebensperger & Loren D. Hayes

8 Rodent sociality: a comparison between caviomorphs and other
   rodent model systems, 201
   Nancy G. Solomon & Brian Keane

9 Cooperation in caviomorphs, 228
   Rodrigo A. Vásquez

10 Caviomorphs as models for the evolution of mating systems in
    mammals, 253
    Emilio A. Herrera

11 Parent-offspring and sibling-sibling interactions in caviomorph
    rodents: a search for elusive patterns, 273
    Zuleyma Tang-Martínez & Elizabeth R. Congdon
12  Fitness consequences of social systems, 306  
   *Loren D. Hayes & Luis A. Ebensperger*

13  An integrative view of caviomorph social behavior, 326  
   *Luis A. Ebensperger & Loren D. Hayes*

   Glossary, 356

   Index, 371
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Introduction

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I.1 Social behavior of caviomorph rodents and book aims

Social behavior involves the actions directed toward, or in response to conspecifics and the fitness consequences for all individuals involved (Wersinger 2009; Székely et al. 2011). Given that social interactions are diverse in nature and extent, social behavior is similarly diverse. Thus, social behavior encompasses a variety of agonistic (including aggressive) behaviors that result in the establishment of dominance hierarchies and territoriality, but also a similarly diverse array of affiliative interactions. Affiliative interactions take place in different contexts, including courtship and other sexual interactions that result in mating systems, parent–offspring interactions that result in parental care patterns, or the relatively permanent association of adult conspecifics that result in sociality (or group-living) and different forms of cooperation.

In the late 1990s and early 2000s, some researchers began to argue that generalizations about rodent social behavior were premature due to the lack of information coming from the caviomorph or New World hystricognath rodents, a socially diverse group of South American rodents (Ebensperger 1998; Tang-Martínez 2003). We propose that a greater focus on caviomorph rodents as subject models of social behavior would contribute greatly to collaborative and integrative research on this area. Caviomorph rodents exhibit a diverse range of social behaviors and life history attributes, and are found in a wide range of habitats. Caviomorphs span from solitary living (Adler 2011) to highly social (Herrera et al. 2011), and live in kin-biased (Lacey & Wieczorek 2004) or non-kin biased (Quirici et al. 2011) groups. Some species provide communal care to offspring (Ebensperger et al. 2007) while others attempt to avoid contact with non-descendant offspring held in communal crèches (Taber & Mcdonald 1992; Campos et al. 2001). Mating systems are equally diverse,
with some species exhibiting monogamy and territoriality, while others exhibit polygyny, or promiscuity (Adrian & Sachser 2011). In terms of life history, caviomorph rodents exhibit a mixture of “fast” and “slow” traits; many have long gestation periods and produce small litters of precocial offspring, yet reach sexual maturity at a young age and exhibit low survival (Kraus et al. 2005). High mortality rates effectively make some species semelparous (Ebensperger et al. 2013). Finally, caviomorph rodents are ecologically diverse, occurring in habitats such as high and low altitude shrublands, tropical and temperate forests, and coastal areas. Habitats range from arboreal to semiaquatic to subterranean. Numerous species have wide geographical ranges, increasing the potential for social and life history flexibility.

Historically, the caviomorph rodents have offered diverse opportunities to studies focused primarily on functional or evolutionary explanations of social behavior. However, caviomorphs are also emerging as good model organisms for integrative research (Colonnello et al. 2011; Ardiles et al. 2013). Researchers have started to make in-roads into the neural mechanisms underlying social variation (e.g. Seidel et al. 2011; Uekita & Okanoya 2011), facilitating comparative analyses that cast mechanism in an evolutionary context (Beery et al. 2008). In some species, we are beginning to understand the neuroendocrine (Ebensperger et al. 2011, 2013) and immunological (Ebensperger et al. 2015) responses to social, reproductive, and environmental conditions. Molecular tools are available for some species, setting the stage for work on sociogenomics and mechanisms underlying reproductive success. Thus, we believe that the time is right to move caviomorph sociobiology into an integrative framework (Hayes et al. 2011). We hope that this book encourages researchers to continue the momentum, increasing the level of international interest in these curious organisms.

The main aim of this book is to provide a comprehensive understanding of caviomorph rodent social systems, focusing on advances and future work in the major themes mentioned above. For each topic addressed in this book we asked contributors to provide relevant information on caviomorph rodents, establish potential parallels (or differences) with other animal models, and place this information into a hypothesis-driven and integrative framework. To the best of our ability, we integrated these individual or topic-based efforts to provide an overall conceptual framework for future studies of social behavior. However, before we introduce these wonderfully diverse and interesting organisms, we first discuss how research approaches to social behavior are evolving. We use this framework to highlight how caviomorph animal models may enrich and contribute to speed up our knowledge on animal social behavior.

I.2 Research approaches to social behavior

Niko Tinbergen’s (1963) seminal paper was pivotal to widening the scope of animal behavior research and encompassing proximate causation (i.e. genetic,
neurological, and hormonal mechanisms), developmental effects, function, and evolution or historical underpinnings of social behavior. Since then, relatively separate lines of research have addressed all four types of questions. In this sense, behavioral ecologists have made great progress to determine the ecological causes and fitness consequences of several aspects of social behavior, including mating systems (Shuster & Wade 2003), parental care (Clutton-Brock 1991; Royle et al. 2012), sociality (Krause & Ruxton 2002), and cooperation (Dugatkin 1997). On the other hand, behavioral geneticists, neurobiologists and endocrinologists have produced information about how genes, gene expression mechanisms, and neuroendocrinological pathways predispose or prone individuals to exhibit different forms of social behavior (e.g. Becker et al. 2002; Anholt & Mackay 2010).

Historically, the ecological-evolutionary work pursued by behavioral ecologists and mechanistic work pursued by geneticists, neurobiologists, and physiologists have followed relatively independent trajectories. Likely, long-term research goals that characterized each field were a major contributor to this end. For example, a large amount of research on the mechanistic underpinnings of social behavior has been based on a few laboratory animal models kept under unnatural conditions and aimed at extrapolations on human-oriented social and sexual behaviors as well as related pathologies (Anholt & Mackay 2010). In contrast, behavioral ecologists have relied on an array of wild animal models and their natural environments, but generally have been less sensitive to the importance of proximate causes (e.g. Krebs & Davies 1993; Davies et al. 2012). As a result, functional and evolutionary implications of behavior from laboratory animal models are complicated, and a lack of detailed genotypic or neuroendocrinological knowledge of wild animal models limits their use to mechanistic studies.

A major push to integrate social behavior research from widely diverse disciplines should be credited to Wilson (1976), who coined the term “sociobiology” to embrace the approach called to examine the biological basis of social behavior. Although Wilson did not develop these issues with great detail in the individual chapters of his seminal book (*Sociobiology: The New Synthesis*, 1976), it was apparent that the aims of sociobiology included genetics, development, and physiological bases of social behavior. Subsequently, behavioral ecologists have highlighted the relevance of mechanisms to fully understand current function and the evolution of social and other behaviors. Thus, mechanisms were placed in a context of constraints and function, with explicit fitness and evolutionary consequences (e.g. Real 1994; Dukas 1998). On the other hand, mechanistically oriented scholars increasingly have shown an explicit interest in placing mechanisms into ecologically and evolutionary relevant settings. This trend is evident from recent reviews and textbooks addressing how genetic, neurological, or endocrinological substrates of social behavior have diverged or converged to explain current within and between species differences in social behavior (e.g. Adkins-Regan 2005; Donaldson & Young 2008; Robinson et al. 2008; Zupanc 2010; O’Connell & Hofmann 2011; Choleris et al. 2013). As a result, we see a growing trend in
Behavioral Ecology and other historically separate disciplines to converge into integrative approaches to explain and predict variation in social behavior (Monaghan 2014). However, what is meant precisely by integrative research?

Tinbergen (1963) suggested that a deep understanding of animal behavior would be achieved through research addressing different, yet complementary perspectives. In practice, this view was a powerful framework to stimulate “multidisciplinarity” (sensu Tress et al. 2004), meaning that disciplines such as behavioral genetics, endocrinology, and behavioral ecology have been focused on similar behavioral traits or phenomena, yet in parallel, keeping multiple disciplinary objectives (Blumstein et al. 2010; Bateson & Laland 2013). Instead, “integration” implies bringing together elements or aspects of multiple disciplines that traditionally have been seen as separate entities. Thus, integration demands “interdisciplinarity” where historically independent disciplines using different methods and approaches converge upon common goals (Tress et al. 2004). More importantly, however, integration in research requires connections and interactions among elements or processes that lie at different biological levels to become explicit (Pigliucci 2003; Perry & Burggren 2007). Identification of these connections should result in an integrated knowledge and new theory about the biological phenomena of interest (Tress et al. 2004). For instance, genomics examines variation associated with complete genomes and aims to understand how this variation interacts with environmental and life history contexts to cause physiological or behavioral differences as emergent outputs (Kültz et al. 2013).

Multidisciplinary approaches to animal behavior are clearly responsible for documenting the extraordinary diverse and complex nature of behavioral phenomena that is evident in almost any textbook on animal behavior or behavioral biology. However, it is this complexity that now demands multidisciplinary approaches to turn interdisciplinary. Interdisciplinary approaches carry the promise to provide integration, implying a clear understanding of how components of underlying mechanisms interact with environmental conditions at different levels to impact an individual's phenotype and fitness (Moore et al. 2011; O’Connell & Hofmann 2011; Hofmann et al. 2014). Several advantages of integrating mechanisms and function are likely to emerge. First, integration expands our knowledge of where information on mechanisms and function are seen as complementary. Second, detailed knowledge of mechanisms may reveal the nature and extent to which mechanisms limit or promote reproductive success, and so contribute to explaining individual and population differences in behavior (e.g. Real 1994; Dukas 1998). Finally, knowledge on mechanisms may highlight novel hypotheses about function, difficult to anticipate without this previous knowledge (e.g. Hennessy et al. 2009; Cirulli et al. 2010).

I.3 Terminology

Social systems include the array of associations and interactions between the sexes, within and outside family bonds. Thus, a complete description of social
systems should include dominance relationships, courtship and intersexual bonds, space use and territoriality, parental care patterns, and the stability of and extent to which adult conspecifics exhibit sociality (i.e. live in groups) and cooperate. While most known organisms exhibit one or more aspects of social behavior, only some social systems include sociality. Other factors such as group composition and the parental care system (uniparental, biparental, communal) play important roles in social system dynamics. These characteristics are not independent of one another. For example, in mammals, there is evidence that particular breeding strategies (one lactating female vs. multiple lactating females in a group) are coupled with particular mating systems (Lukas & Clutton-Brock 2012), and one potential advantage of group-living is that individuals can collectively defend a territory. Thus, a challenge to studying social systems is determining the distinctions—and links—between these different components. In this book, contributors will use terms like sociality or group-living, breeding strategies, and mating systems to describe different aspects of caviomorph rodent social systems. Below, we define these key terms (see the Glossary for a complete list of terms, highlighted in bold on their first occurrence throughout the book).

I.3.1 Sociality (or group-living)
Sociality or group-living involves spatial and temporal proximity of group members that results from a mutual attraction to conspecifics rather than from attraction to a same resource or physical condition (Parrish et al. 1997; Krause & Ruxton 2002). Animal groups range from short-term to relatively long-term associations (Parrish et al. 1997) and this variation is determined in part by the strength to which group members are attracted to each other (i.e. an intrinsic factor). Temporal duration and emerging group stability are also influenced by ecological conditions that limit the ability of individuals of living independently (Emlen 1995), or by demographic processes linked to mortality (Ebensperger et al. 2009). Sociality is usually defined based on the degree of the spatial overlap of individuals (Krause & Ruxton 2002) and quantified based on the total number of individuals in a group (e.g. group size). Researchers also use metrics that account for the extent of socially affiliative interactions within groups (e.g. social bonding). Recent advances in social network theory (Whitehead 2008) have improved our ability to incorporate both spatial and behavioral interactions in sociality metrics (e.g. Wey et al. 2013).

I.3.2 Mating systems and parental care
An animal’s mating system involves the association between males and females during breeding activity, and includes the relative effort of males and females in parental care (Bolhuis & Giraldeau 2005). Parental care in turn involves behaviors (and other forms of investment) exhibited by parents that increase the survival and condition of their offspring, typically at a cost to their own fitness (Royle et al. 2012). Thus, mating systems are characterized by the number of
sexual partners that individual male and females have, and the extent to which parental care is shared between both sexes. **Monogamy** occurs when one member of each sex breeds together as a pair either serially or over a lifetime. In **polygynous** systems, males mate with multiple females, defending the females (female-defense polygyny) or resources (resource-defense polygyny) that they use. **Promiscuity** characterizes systems in which males and females mate multiply. Rarely, a species is polyandrous, a system in which multiple males mate with one female. In reality, mating systems are more complex and include two components—social and genetic. The social mating describes the associative behavior of individuals (e.g. whether individuals remain in pairs). In contrast, genetic mating systems describe the reproductive outcomes of the behavior. It is well known that “cheating” occurs, resulting in genetic mating systems that differ from the social mating system (Birkhead & Møller 1992).

Parental care strategies are typically defined based on the numbers of parents providing care to offspring. In monogamous species, males and females typically share parental care duties similarly, referred to as biparental care. In contrast, females are typically the main providers of parental care in most other mating systems. In some species, females are the only care-givers (uniparental care) whereas in others multiple females care for offspring in communal litters or crèches (communal care).

### I.3.3 Territoriality and dominance hierarchies

**Territoriality** occurs when one individual or groups of individuals prevent conspecifics or members of other groups gaining access to a proportion of their range areas. Typically, territory defense results in exclusive access to the resources (e.g. food, refuges) within the defended area at the expense of energetic and time costs involved in such defense (Maher & Lott 1995). The motivation for territoriality may differ between the sexes. For example, in some social mammals (e.g. house mice, *Mus musculus*), males defend territories including groups of communal females while females communally defend litters from intruder males (Manning et al. 1995). It seems important here to note that territorial animals may exclude conspecifics from an area with the use of a combination of social interactions, including direct fight and chases, and scent markings.

In social species, agonistic interactions between individuals may result in **dominance hierarchies** (Drews 1993; Pusey & Packer 1997). Dominance relationships in social systems are important because these relationships determine the rank and therefore, priority of access of individuals to critical resources (and its effects on condition). In addition, social rank in some social species determines the extent to which each individual contributes with direct reproduction and offspring care. Dominance relationships can also affect the stability of groups, possibly explaining the evolution of fission–fusion societies with high rates of group membership turnover.
Hierarchies can range from linear associations (pecking-order) characterized by transitive relationships, to more complex associations characterized by intransitive relationships (Earley & Dugatkin 2010). Regardless, rank may be influenced by intrinsic factors, including body size, weaponry, or age. In addition, hierarchies are determined by motivational factors such as energy reserves, residency or tenure, or experience during previous contests (Pusey & Packer 1997; Broom et al. 2009; Earley & Dugatkin 2010).

I.3.4 Cooperation and breeding strategies

Different forms of cooperation may evolve once individuals live in groups, including cooperative hunting, communal breeding, or social inspection of predators (Dugatkin 1997). We restrict the use of cooperation to social interactions that result in net inclusive fitness benefits to all participants. Theoretically, cooperation can evolve through several mechanisms, including kin selection, reciprocity, by-product mutualism, or trait (group) selection (Dugatkin 1997). Here, we follow Dugatkin (1997) in that individuals behave in a manner that makes cooperation possible. Thus, different aspects of social behavior may result in cooperation, including individual coordination to scan for approaching predators, coordination during group foraging to locate and attain patchily distributed food resources, or communal defense of a territory.

In addition, cooperation may result in different “breeding strategies,” meaning that the degree to which direct reproduction and parental effort are shared (reproductive skew) within groups may vary (Brown 1987; Hayes 2000; Silk 2007). Usually, researchers refer to the breeding status of females and communal care (or allopasternal care) of non-breeders in groups, a distinction that unless otherwise stated, will be made in this book. Singular breeding is a strategy in which groups consist of one or a few reproductive females, one or more breeding males (i.e. high reproductive skew) and non-breeders that provide allopasternal care to non-descendant offspring (Brown 1987; Silk 2007). Plural breeding is a strategy in which multiple females (and males) in the same social group breed (i.e. low reproductive skew). Plural breeding may occur with and without communal care of offspring (Silk 2007). In some insects and very few mammals, social groups consist of distinct classes, including a reproductive female, one or more reproductive males and non-breeders (Wilson 1976), a condition referred to as eusociality.

Other researchers have used the terms cooperative breeders, communal breeders, and social breeders, which are based on the types of cooperation or care provided to offspring, to describe the breeding structure of mammals (Lukas & Clutton-Brock 2012). In this scheme, cooperative breeders are species in which a proportion of females do not breed regularly and provide allopasternal care to non-descendant offspring. Communal breeders are species in which most adult females breed and rear offspring communally. Social breeders are species in
Introduction

which females live in groups, but do not rear offspring communally or cooperate. In this chapter, we use Silk’s (2007) classification scheme, which includes singular breeders and plural breeders with and without communal care. Thus, singular breeders are the same as cooperative breeders, plural breeders with communal care are the same as communal breeders and plural breeders without communal care are the same as social breeders (Silk 2007; Lukas & Clutton-Brock 2012).

1.4 Structure of the book

We aim to provide relevant information on caviomorph rodent social systems, establish potential parallels (or differences) with other animal models, and place this information into a hypothesis-driven and integrative framework. To this end, the book includes contributions from experts on mechanistic and functional aspects of social behavior. In Chapter 1, Ojeda et al. describe the general biology of caviomorph rodents with an emphasis on geographic distribution, life history, life styles, ecology, and evolutionary history. This chapter provides a context for readers interested in social behavior but not familiar with rodents. In Chapter 2, Maher and Burger highlight how caviomorph social systems vary within and across species. These authors relate species variation to differences in ecological lifestyles, including diet, habitat mode, space use, and activity period. Within species variation seem linked to differences in resource distribution, predation risk, or population density. They highlight how the uniqueness of these social systems offer potentially fruitful lines for future research. In Chapter 3, Beery et al. address the neural underpinnings of different aspects of social behavior, with the aim to provide a basis to explain (predict) intra- and inter-species variation in conspecific tolerance, conspecific seeking propensity, partner preference, or extent of parental care in current day forms. In Chapter 4, Colonnello et al. provide a developmental background and take current laboratory-based studies to examine the strength of social bonds, sensitivity to social environment, and the developmental and epigenetic factors involved in the expression of social behavior. In Chapter 5, Lacey examines the proximate and functional causes, and its consequences on social and genetic structure of species, with an emphasis on caviomorph rodents. In Chapter 6, Francescoli et al. review the different modalities of communication that evolved in caviomorph rodents. The chapter investigates how the use of different communication modalities (chemical, visual, auditory) and complexity may be further influenced by group living. In Chapter 7, Ebensperger and Hayes examine how ecological and life-history factors explain current sociality and have driven this aspect of social behavior in caviomorphs. This chapter highlights how studies on caviomorphs add to the multi-dimensional nature of variation in sociality. Solomon and Keane dedicate Chapter 8 to discussing some problems with trying to define and quantify sociality. Then, these authors examine some of the ultimate hypotheses proposed to explain sociality in rodents to highlight how
the study of caviomorphs is likely to provide independent tests of hypotheses for theory based on non-caviomorph rodents. In Chapter 9, Vásquez addresses how social behavior traits of caviomorphs are potentially cooperative, and how different evolutionary mechanisms may explain them. Herrera leads Chapter 10 to examine how mating systems vary across caviomorphs, and the extent to which this variation reflects ecological factors and phylogeny. Tang-Martínez and Congdon use Chapter 11 to provide an update on what is known about parent–offspring and sibling–sibling relationships in caviomorphs. These authors want the chapter to highlight relationships among these social traits, life history traits (e.g. levels of precociality), and life styles (e.g. fossoriality). The next chapter is a review by Hayes and Ebensperger, and reveals how little we know about the fitness consequences of group living in caviomorphs. However, Chapter 12 also shows how fitness effects of group-living vary across the few better-known species. In Chapter 13, Ebensperger and Hayes integrate major themes from previous chapters and provide an explicit integrative framework for future studies of social behavior.

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References

Introduction


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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 Pas- cual (1972) noted, these proto-caviomorphs, found a vacuum leading to rapid
diversification in the early Oligocene, when “it is already possible to recognize all four caviomorph superfamilies” (p. 278).

The four superfamilies, Cavioida, Chinchilloidea, Erethizontoidea, and Octodontoidea include 13 families, 56 genera and 246 extant species (Upham & Patterson 2012). The superfamily Cavioida includes the Dasyproctidae (agouties), Cuniculidae (papas), 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 Cavioida + 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 Cavioida/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 throughout 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).