

Thales Renato Ochotorena de Freitas
Gislene Lopes Gonçalves
Renan Maestri *Editors*

Tuco-Tucos

An Evolutionary Approach
to the Diversity of a Neotropical
Subterranean Rodent

Tuco-Tucos

Thales Renato Ochotorena de Freitas
Gislene Lopes Gonçalves • Renan Maestri
Editors

Tuco-Tucos

An Evolutionary Approach to the Diversity
of a Neotropical Subterranean Rodent

 Springer

Editors

Thales Renato Ochotorena de Freitas
Department of Genetics
Federal University of Rio Grande do Sul
Porto Alegre, Rio Grande do Sul, Brazil

Gislene Lopes Gonçalves
Department of Genetics
Federal University of Rio Grande do Sul
Porto Alegre, Rio Grande do Sul, Brazil

Renan Maestri
Department of Ecology
Federal University of Rio Grande do Sul
Porto Alegre, Rio Grande do Sul, Brazil

ISBN 978-3-030-61678-6 ISBN 978-3-030-61679-3 (eBook)
<https://doi.org/10.1007/978-3-030-61679-3>

© Springer Nature Switzerland AG 2021

This work is subject to copyright. All rights are reserved by the Publisher, whether the whole or part of the material is concerned, specifically the rights of translation, reprinting, reuse of illustrations, recitation, broadcasting, reproduction on microfilms or in any other physical way, and transmission or information storage and retrieval, electronic adaptation, computer software, or by similar or dissimilar methodology now known or hereafter developed.

The use of general descriptive names, registered names, trademarks, service marks, etc. in this publication does not imply, even in the absence of a specific statement, that such names are exempt from the relevant protective laws and regulations and therefore free for general use.

The publisher, the authors, and the editors are safe to assume that the advice and information in this book are believed to be true and accurate at the date of publication. Neither the publisher nor the authors or the editors give a warranty, expressed or implied, with respect to the material contained herein or for any errors or omissions that may have been made. The publisher remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

This Springer imprint is published by the registered company Springer Nature Switzerland AG
The registered company address is: Gewerbestrasse 11, 6330 Cham, Switzerland

Foreword

The tucotuco (Ctenomys brasiliensis) is a curious small animal, which may be briefly described as a Gnawer, with the habits of a mole.

Charles Darwin

The Voyage of the Beagle

Chapter III, Maldonado

Such begin Darwin's comments on tuco-tucos, based on his encounters with these animals along the southern coast of Uruguay. Now, 175 years after the original publication of Darwin's observations, biologists continue to be fascinated by these charismatic rodents. In part, this interest reflects the somewhat mysterious nature of tuco-tucos—even in areas where the animals are locally abundant and can at times be heard calling from all directions, it is often challenging to catch a glimpse of these largely subterranean mammals. Increasingly, though, interest in tuco-tucos reflects our growing understanding of the biology of these animals and the unexpected wealth of phenotypic and genotypic variation that they represent. Indeed, as evident from the contents of this volume, studies of tuco-tucos now encompass analyses of systematic, phylogenetic, morphological, physiological, ecological, and behavioral diversity, providing important opportunities to examine the evolutionary processes underlying divergence within *Ctenomys* and, concomitantly, convergence between these and other lineages of subterranean rodents.

One attribute of tuco-tucos that makes them both intriguing and at times challenging to study is the apparently rapid divergence of species within the genus *Ctenomys*. As Diego Verzi and colleagues indicate (Chap. 1), while the family Ctenomyidae appears to date to the Oligocene, the single extant genus *Ctenomys* has arisen much more recently, with current species-level diversification dating only to the early Pleistocene. This rapid burst of speciation has made it difficult to evaluate the evolutionary relationships among species, as molecular genetic analyses have often failed to reveal much phylogenetic structure, particularly for deeper nodes within the genus. Indeed, as Guillermo D'Elía and co-authors state (Chap. 2), phylogenetic analyses of tuco-tucos are in many ways still in their infancy and will benefit substantially from inclusion of additional data sets (e.g., genomic-level sequencing) as well as more comprehensive sampling of putative species and

species groups. At the same time, the rapid diversification within *Ctenomys* creates exciting opportunities to explore the evolutionary mechanisms underlying speciation in this lineage. The role of chromosomal rearrangements in promoting speciation has been a particular focus for studies of tuco-tucos due to the often pronounced karyotypic differences among species, including those for which molecular genetic analyses fail to detect marked differentiation. This theme is examined by Thales de Freitas (Chap. 3), who concludes that evidence for distinct processes of speciation (e.g., allopatric, sympatric, chromosomal) varies in relation to the time since divergence among different members of the genus *Ctenomys*.

Geographically, tuco-tucos are widespread, occurring throughout much of sub-Amazonian South America. At the level of individual taxa, however, it has long been thought that allopatry dominates, with only a few examples of sympatry having been identified within *Ctenomys*. To explore how local spatial relationships among species translate into the genus-level distribution of these animals, Renan Maestri and Bruce Patterson (Chap. 4) characterize geographic variation in several attributes of *Ctenomys*, including patterns of species richness and range size. These authors report that although species ranges tend to be smaller in *Ctenomys*, the exclusivity of these ranges does not differ from that observed in other lineages of caviomorph rodents, providing no evidence that allopatry is particularly pronounced among tuco-tucos. Fernando Mapelli and colleagues (Chap. 5) add a genetic component to analyses of geographic variation, arguing that landscape features may impact the demographic processes that shape patterns of genetic differentiation within and among species of *Ctenomys*. Their review suggests that landscape-level genetic variation reflects a baseline pattern of isolation by distance that is modified by a complex, species-specific interplay between geographic features, environmental conditions, and demographic parameters.

In terms of their gestalt, it has been suggested that if you have seen one tuco-tuco, you have seen them all. This quip reflects the general expectation that the challenges associated with life in underground burrows have acted to constrain morphological and other forms of phenotypic diversification within *Ctenomys*. As knowledge of these animals has increased, it has become increasingly apparent that they are more phenotypically diverse than has been appreciated. Morphologically, variation is evident for multiple cranial traits, and, as reported by Rodrigo Fornel and co-authors (Chap. 6), this variation displays geographic but not phylogenetic signal, suggesting that environmental conditions may play a critical role in shaping skull structure in these animals. One obvious environmental factor that may contribute to this variation is the difference in the soils in which the animals live. As described by Aldo Vassallo and colleagues (Chap. 7), although tuco-tucos rely primarily on their forepaws to dig, they also routinely use their incisors to chew through obstructions or loosen hard chunks of soil. Accordingly, the structure of both the forelimbs and the skull may vary with soil type, and, conversely, constraints on the biomechanics of digging may preclude the animals from occupying particular soils. Soil may also be an important determinant of the underappreciated variation in pelage coloration that occurs within *Ctenomys*. Using comparisons of overall pelage color as well as the structure of individual hairs, Gislene Goncalves (Chap. 8) argues

that differences in coloration among species of tuco-tucos from the Atlantic coasts of Brazil and Argentina reflect selection imposed by differences in soil color, with color matching to local substrates serving to protect animals from predation while active on the surface.

Interactions between individuals and their environments are also central to studies of the ecology and physiology of *Ctenomys*. The role of tuco-tucos as ecosystem engineers is examined by Bruno Kubiak and Daniel Gailano (Chap. 9), who also consider the effects of habitat parameters on species' distributions as well as spatial and social relationships among conspecifics. Although relevant data are lacking for many species, the emerging picture is one of greater than expected ecological and behavioral variation within the genus. One critical aspect of a species' ecology is its diet, which can affect not only where animals occur on the landscape but also how they acquire energy and nutrients, thereby providing a particularly direct link between external conditions and intrinsic processes. Although all tuco-tucos are herbivorous, surprisingly few detailed studies of the animals' diets have been conducted. As Carla Lopes (Chap. 10) reports, the growing use of DNA sequencing of fecal samples to characterize diets is creating new opportunities to examine dietary variation within and among members of the genus *Ctenomys*, including the role of diet partitioning in shaping the few examples of sympatry that have been reported for these animals. Maria Sol Fanjul and colleagues (Chap. 11) explore the inner workings of tuco-tucos in greater detail, revealing how differences in habitat conditions as well as differences in how individuals use their habitats contribute to adaptively important variation in multiple physiological systems, including processing of sensory information, response to external stressors, and regulation of both water and energy balance. Extrinsicly generated differences in physiology may be mediated by variation in individual phenotypes (e.g., sex, reproductive status), thereby adding an additional layer of complexity to efforts in understanding how external conditions shape the internal biology of tuco-tucos. In the final chapter of the volume, Cristina Matzenbacher and Juliana da Silva (Chap. 12) take a more applied approach to interactions between tuco-tucos and their environments by examining the role of these animals as bioindicators of environmental change, specifically the introduction of heavy metals and other toxic compounds as a result of human activity. More generally, this discussion raises the issue of conservation of the genus *Ctenomys*, thereby serving to connect the previous chapters to the increasingly important need to ensure that members of this lineage are protected from an ever-growing list of threats.

In closing, one theme that resonates throughout this volume is diversity. From systematic and phylogenetic revisions of *Ctenomys* to analyses of interactions between the environment and specific physiological processes, it is clear that studies of tuco-tucos are revealing new and sometimes unexpected patterns of diversification in this relatively young clade of rodents. Coupled with an ever-growing suite of analytical tools, this diversity creates novel opportunities to examine long-standing questions regarding the biology of tuco-tucos. For example, efforts to understand the often marked karyotypic differences among otherwise closely related species should benefit from the use of genomic tools to identify the specific portions

of the genome that are impacted by chromosomal rearrangements. Similarly, as our ability to characterize the genomic architecture of specific phenotypic traits increases, we will be better able to examine the genetic bases for adaptive traits such as the specialized morphological features associated with digging. More generally, the expanding catalog of diversity within *Ctenomys* means that members of this genus are increasingly recognized as important models for research on a wide range of evolutionary topics, including studies that explore the effects of pathogen communities on immunological function or the role of ecological factors in generating interspecific differences in social systems. All told, our growing understanding of the biology of tuco-tucos suggests that the “curious small animals” that intrigued Darwin will continue to play a central role in biological research for years to come.

Berkeley, USA

Eileen Lacey

Introduction

This book examines the biology of tuco-tucos (*Ctenomys*) from an evolutionary perspective. *Ctenomys* is a remarkable lineage of subterranean rodents widely distributed over the southern half of South America. It exhibits various adaptations for living underground—mostly solitarily, but in some species also in social groups. Such a peculiar lifestyle has long attracted the attention of scientists, including Charles Darwin. In 1832, during the voyage of the Beagle, Darwin had a memorable experience with tuco-tucos when he stayed in Maldonado, Uruguay, which he registered in his diary (published in 1839).

The next century of scientific studies of *Ctenomys* was mostly limited to species descriptions obtained on European expeditions to South America. Beginning in 1950, a wealth of knowledge on physiology, ecology, genetics, morphology, paleontology, and taxonomy has been documented in scientific journals, as well as in many theses and dissertations dedicated to this intriguing group. Most studies have documented local or regional patterns shown by tuco-tucos; however, global or comprehensive synopses are still needed. We seek to partly fill this gap by inviting investigators that have worked for years both in field and laboratory with extinct and extant tuco-tuco species to review major evolutionary topics and frame these essays with the breadth of current understanding. We hope that the combination of extensive reviews and original information on tuco-tucos, produced by numerous authors, will stimulate future studies.

Among the subterranean rodents, the tuco-tucos (*Ctenomys*) stand along with the Mediterranean mole rats (*Spalax*), North American pocket gophers (*Thomomys* and *Geomys*), and species of Bathyergidae in Africa as the major lineages well-known from long-standing studies. If one considers that tuco-tucos are endemic to the Neotropics—where funding for basic research is limited—the status of knowledge reached for *Ctenomys* is remarkable, resulting from the efforts and passion of many individuals.

With some frequency—before we decide for this book project—we used to ask colleagues during annual scientific meetings if they wonder what maintains the passion for tuco-tucos across distinct generations of scientists (since Darwin) and, particularly, what makes *Ctenomys* an exciting group to be studied. In general, people

mentioned that when tuco-tucos are carefully observed in the field, enormous variation is found, such as in their behavior, pelage, skull, and digging ability. The facilities of working with this group, as in the capture of specimens in the field and the possibility of keeping them in captivity, and locating their populations and tracking them in time and space for long years, together with the underlying variation in a rodent that seems uniform, were considered, in a large degree, the triggers for maintaining the passion for tuco-tucos. While compiling background and putting them into context, it became clear—at least explicit—why tuco-tucos are fascinating from an evolutionary perspective, and we felt motivated to organize this volume.

Considering that the articles on *Ctenomys* started from the 1950s of the last century, we believe that there is currently sufficient data spread over various disciplines and well-established lines of research that, after 70 years, should be put in a book trying to make a synthesis of what already exists. We should mention previous books that included *Ctenomys*, starting with *Evolution of Subterranean Mammals at the Organismal and Molecular Levels*, edited by Eviatar Nevo and Oswaldo A. Reig, which included a whole chapter about the genus from an evolutionary point of view (Reig et al. 1990). The genus also appeared on books that featured subterranean rodents such as *Life Underground: The biology of subterranean rodents* (2000), authored by Eileen Lacey, James L. Patton, and Guy N. Cameron, and more recently, in 2010, the book *Subterranean Rodents: News from Underground*, by Sabine Gegall, Hynek Burda, and Cristian E. Schleich. Given how much the scientific community has learned about tuco-tucos since Reig et al. (1990), we believe it is time for *Ctenomys* to have their own book.

Species and local populations of tuco-tucos are the most interesting South American mammals for studying mechanisms underlying speciation. Basically, two principal interconnected aspects drive interest in tuco-tucos: chromosomes and species diversity. *Ctenomys* form one of the most karyotypically diverse clades known in mammals, with chromosomal diploid numbers ranging from 10 to 70 (Cook et al. 1990; Gallardo 1991; Reig et al. 1992; Ortells 1995). In addition, 65 species are recognized for the genus (Teta and D'Elia 2020, Chap. 2, this volume), more than any other group of subterranean rodents (Reig et al. 1990; Lessa and Cook 1998; Castillo et al. 2005; Woods and Kilpatrick 2005). Since *Ctenomys* appeared in the late Pliocene, their extant diversity was achieved by remarkable flurry of speciation events (Verzi et al. 2010; Parada et al. 2011). The age of the genus is quite recent, estimated at ca. 5 Ma according to molecular evidence (Parada et al. 2011; Upham and Patterson 2015), which agrees with the paleontological records (Verzi 1999, 2002; Verzi et al. 2010; Chap. 1, this volume).

Reig and Kiblicky (1969) were the first to propose that tuco-tucos are a prime example of chromosomal speciation. Reig et al. (1990) raised the idea, still accepted, that diversification may have been facilitated by the isolation of small demes that characterize population structure in most species and extensive chromosomal rearrangements (Reig and Kiblicky 1969; Cook et al. 1990; Gallardo 1991; Ortells 1995). In fact, the high intra- and interspecific chromosomal polymorphisms—once suggested as the main factor responsible for fast speciation of *Ctenomys* (Ortells 1995)—do not seem to be directly responsible for its species richness. Thus, rather

than a triggering speciation in tuco-tucos, chromosomal rearrangements speed up the process by modulating gene flow rate in certain genome regions (Torgasheva et al. 2017), suggesting an even more complex scenario for cladogenesis.

The collection of chapters in this book articulates research views that are disseminated across major subjects as paleontology, systematics, evolutionary ecology, and genetics. To address such a broad range of topics from the perspective of a single mammal genus is unusual and transcends good-study-model reasoning. Such excess might be based on subjective aspects of tuco-tucos since it is a charismatic animal, which typically touches human feelings, including those from contributors and readers.

We are most grateful to the authors for their willingness to join us and make this book happen. Many thanks are also due to Eileen Lacey for writing the foreword and offering editorial suggestions, as well as to Bruce D. Patterson for helpful comments on our Introduction. We thank Springer Nature Publisher for bringing our project in the current form, particularly Luciana Christante de Mello, Vignesh Viswanathan, and Nolan Mallaigh, for their editorial assistance.

Porto Alegre, Rio Grande do Sul, Brazil Thales Renato Ochotorena de Freitas
 Gislene Lopes Gonçalves
 Renan Maestri

Literature Cited

- Castillo AH, Cortinas MN, Lessa EP (2005) Rapid diversification of South American tuco-tucos (*Ctenomys*; Rodentia, Ctenomyidae): Contrasting mitochondrial and nuclear intron sequences. *J Mammal* 86:170–179
- Cook JA, Anderson S, Yates TL (1990) Notes on Bolivian Mammals 6: the Genus *Ctenomys* (Rodentia, Ctenomyidae) in the Highlands. *Am Mus Novit* 2980:1–27
- Gallardo MH (1991) Karyotypic evolution in *Ctenomys* (Rodentia, Ctenomyidae). *J Mammal* 72:1–21
- Lessa EP, Cook JA (1998) The molecular phylogenetics of tuco-tucos (genus *Ctenomys*, Rodentia: Octodontidae) suggests an early burst of speciation. *Mol Phylogenet Evol* 9:88–99
- Ortells MO (1995) Phylogenetic analysis of G-banded karyotypes among the South American subterranean rodents of the genus *Ctenomys* (Caviomorpha: Octodontidae), with special reference to chromosomal evolution and speciation. *Biol J Linnean Soc* 54:43–70
- Parada A, D’Elia G, Bidau CJ, Lessa EP (2011) Species groups and the evolutionary diversification of tuco-tucos, genus *Ctenomys* (Rodentia: Ctenomyidae). *J Mammal* 92: 671–682
- Reig OA, Kiblisly P (1969) Chromosome multiformity in the genus *Ctenomys* (Rodentia, Octodontidae). *Chromosoma* 28:211–244
- Reig O, Busch C, Contreras J, Ortells M (1990) An overview of evolution, systematic, population biology and molecular biology. In: Nevo E, Reig OA (eds) *Biology of Subterranean mammals*. Wiley-Liss, New York, pp 71–96
- Reig O, Massarini A, Ortells M, Barros M, Tiranti S, Dyzenchouz F (1992) New karyotypes and C-banding patterns of the subterranean rodents of the genus *Ctenomys* (Caviomorpha, Octodontidae) from Argentina. *Mammalia* 56:603–624

- Teta P, D'Elia G (2020) Uncovering the species diversity of subterranean rodents at the end of the World: three new species of Patagonian tuco-tucos (Rodentia, Hystricomorpha, *Ctenomys*). PeerJ 8:e9259
- Torgasheva AA, Basheva EA, Gómez Fernández MJ, et al (2017) Chromosomes and speciation in tuco-tuco (*Ctenomys*, Hystricognathi, Rodentia). Russ J Genet Appl Res 7:350–357
- Upham NS, Patterson, BD (2015) Evolution of caviomorph rodents: a complete phylogeny and timetree for living genera. Biology of Caviomorph Rodents: Diversity and Evolution 1:63–120
- Verzi DH, Olivares AI, Morgan CC (2010) The oldest South American tuco-tuco (late Pliocene, northwestern Argentina) and the boundaries of the genus *Ctenomys* (Rodentia, Ctenomyidae). Mamm Biol 75:243–252
- Verzi DH (2002) Patrones de evolución morfológica en Ctenomyinae (Rodentia, Octodontidae). Mastozool Neotrop 9:309–328
- Verzi DH (1999) The dental evidence on the differentiation of the ctenomyine rodents (Caviomorpha, Octodontidae, Ctenomyinae). Acta Theriologica 44:263–282
- Woods C Kilpatrick C (2005) Infraorder Hystricognathi Brandt, 1855. In: Mammal species of the world: a taxonomic and geographic reference, vol 2, 3rd edn. pp 1538–1600

Contents

Part I Evolution of *Ctenomys*

- 1 The History of *Ctenomys* in the Fossil Record: A Young Radiation of an Ancient Family** 3
Diego H. Verzi, Nahuel A. De Santi, A. Itatí Olivares,
Cecilia C. Morgan, and Alicia Álvarez
- 2 A Short Overview of the Systematics of *Ctenomys*: Species Limits and Phylogenetic Relationships** 17
Guillermo D'Elía, Pablo Teta, and Enrique P. Lessa
- 3 Speciation Within the Genus *Ctenomys*: An Attempt to Find Models** 43
Thales Renato Ochotorena de Freitas

Part II Geographic Patterns

- 4 Geographical and Macroecological Patterns of Tuco-Tucos** 69
Renan Maestri and Bruce D. Patterson
- 5 Phylogeography and Landscape Genetics in the Subterranean Rodents of the Genus *Ctenomys*** 83
Fernando Javier Mapelli, Ailin Austrich, Marcelo Javier Kittlein,
and Matías Sebastián Mora

Part III Organismal Biology

- 6 Skull Shape and Size Diversification in the Genus *Ctenomys* (Rodentia: Ctenomyidae)** 113
Rodrigo Fornel, Renan Maestri, Pedro Cordeiro-Estrela,
and Thales Renato Ochotorena de Freitas

7 Biomechanics and Strategies of Digging 141
 Aldo I. Vassallo, Federico Becerra, Alejandra I. Echeverría,
 Guido N. Buezas, Alcira O. Díaz, M. Victoria Longo,
 and Mariana Cohen

8 Adaptive Pelage Coloration in *Ctenomys* 167
 Gislene Lopes Gonçalves

Part IV Environmental Relationships

**9 Environmental and Ecological Features of the Genus
*Ctenomys*** 193
 Daniel Galiano and Bruno Busnello Kubiak

10 The Diet of *Ctenomyids* 213
 Carla Martins Lopes

11 Ecological Physiology and Behavior in the Genus *Ctenomys* 221
 María Sol Fanjul, Ana Paula Cutrera, Facundo Luna,
 Cristian E. Schleich, Valentina Brachetta, C. Daniel Antenucci,
 and Roxana R. Zenuto

**12 Effects of Environmental Pollution on the Conservation
 of *Ctenomys*** 249
 Cristina A. Matzenbacher and Juliana da Silva

Index 265

Contributors

Alicia Álvarez Instituto de Ecoregiones Andinas, CONICET, Jujuy, Argentina

C. Daniel Antenucci Grupo ‘Ecología Fisiológica y del Comportamiento’, Instituto de Investigaciones Marinas y Costeras, Universidad Nacional de Mar del Plata, Consejo Nacional de Investigaciones Científicas y Técnicas, Mar del Plata, Argentina

Ailin Austrich Departamento de Biología, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, Instituto de Investigaciones Marinas y Costeras (IIMyC), CONICET – UNMdP, Mar del Plata, Buenos Aires, Argentina

Federico Becerra Grupo Morfología Funcional y Comportamiento, Instituto de Investigaciones Marinas y Costeras (IIMyC, UNMDP-CONICET), Universidad Nacional de Mar del Plata (UNMdP), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Mar del Plata, Buenos Aires, Argentina

Valentina Brachetta Grupo ‘Ecología Fisiológica y del Comportamiento’, Instituto de Investigaciones Marinas y Costeras, Universidad Nacional de Mar del Plata, Consejo Nacional de Investigaciones Científicas y Técnicas, Mar del Plata, Argentina

Guido N. Buezas Grupo Morfología Funcional y Comportamiento, Instituto de Investigaciones Marinas y Costeras (IIMyC, UNMDP-CONICET), Universidad Nacional de Mar del Plata (UNMdP), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Mar del Plata, Buenos Aires, Argentina

Mariana Cohen Grupo Histología e Histoquímica, Instituto de Investigaciones Marinas y Costeras (IIMyC, UNMDP-CONICET), Universidad Nacional de Mar del Plata (UNMdP), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Mar del Plata, Buenos Aires, Argentina

Pedro Cordeiro-Estrela Departamento de Sistemática e Ecologia, Centro de Ciências Exatas e da Natureza – Campus I, Universidade Federal da Paraíba, Jardim Universitário s/n, João Pessoa, PB, Brazil

Ana Paula Cutrera Grupo ‘Ecología Fisiológica y del Comportamiento’, Instituto de Investigaciones Marinas y Costeras, Universidad Nacional de Mar del Plata, Consejo Nacional de Investigaciones Científicas y Técnicas, Mar del Plata, Argentina

Juliana da Silva Universidade LaSalle – UNILASALLE and Universidade Luterana do Brasil - ULBRA, Canoas, RS, Brazil

Thales Renato Ochotorena de Freitas Department of Genetics, Federal University of Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brazil

Nahuel A. De Santi Sección Mastozoología, CONICET, Museo de La Plata, La Plata, Argentina

Guillermo D’Elía Instituto de Ciencias Ambientales y Evolutivas, Universidad Austral de Chile, Valdivia, Chile

Alcira O. Díaz Grupo Histología e Histoquímica, Instituto de Investigaciones Marinas y Costeras (IIMyC, UNMDP-CONICET), Universidad Nacional de Mar del Plata (UNMDP), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Mar del Plata, Buenos Aires, Argentina

Alejandra I. Echeverría Grupo Morfología Funcional y Comportamiento, Instituto de Investigaciones Marinas y Costeras (IIMyC, UNMDP-CONICET), Universidad Nacional de Mar del Plata (UNMDP), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Mar del Plata, Buenos Aires, Argentina

María Sol Fanjul Grupo ‘Ecología Fisiológica y del Comportamiento’, Instituto de Investigaciones Marinas y Costeras, Universidad Nacional de Mar del Plata, Consejo Nacional de Investigaciones Científicas y Técnicas, Mar del Plata, Argentina

Rodrigo Fornel Programa de Pós-Graduação em Ecologia, Departamento de Ciências Biológicas, Universidade Regional Integrada do Alto Uruguai e das Missões – Campus de Erechim, Erechim, RS, Brazil

Daniel Galiano Laboratório de Zoologia, Universidade Federal da Fronteira Sul, Realeza, Brazil

Gislene Lopes Gonçalves Departamento de Genética, Universidade Federal do Rio Grande do Sul, Porto Alegre, RS, Brazil

Departamento de Recursos Ambientales, Facultad de Ciencias Agronómicas, Universidad de Tarapacá, Arica, Chile

Marcelo Javier Kittlein Departamento de Biología, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, Instituto de Investigaciones Marinas y Costeras (IIMyC), CONICET – UNMDP, Mar del Plata, Buenos Aires, Argentina

Bruno Busnello Kubiak Programa de Pós-Graduação em Genética e Biologia Molecular, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil

Enrique P. Lessa Departamento de Ecología y Evolución, Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay

M. Victoria Longo Grupo Histología e Histoquímica, Instituto de Investigaciones Marinas y Costeras (IIMyC, UNMDP-CONICET), Universidad Nacional de Mar del Plata (UNMDP), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Mar del Plata, Buenos Aires, Argentina

Carla Martins Lopes Departamento de Biodiversidade e Centro de Aquicultura, Instituto de Biociências, Universidade Estadual Paulista (UNESP), Rio Claro, SP, Brazil

Facundo Luna Grupo ‘Ecología Fisiológica y del Comportamiento’, Instituto de Investigaciones Marinas y Costeras, Universidad Nacional de Mar del Plata, Consejo Nacional de Investigaciones Científicas y Técnicas, Mar del Plata, Argentina

Renan Maestri Departamento de Ecologia, Universidade Federal do Rio Grande do Sul, Porto Alegre, RS, Brazil

Fernando Javier Mapelli División Mastozoología, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Ciudad Autónoma de Buenos Aires, Argentina

Cristina A. Matzenbacher Programa de Pós-Graduação em Genética e Biologia Molecular, Universidade Federal do Rio Grande do Sul - UFRGS, Porto Alegre, Brazil

Matías Sebastián Mora Departamento de Biología, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, Instituto de Investigaciones Marinas y Costeras (IIMyC), CONICET – UNMDP, Mar del Plata, Buenos Aires, Argentina

Cecilia C. Morgan Sección Mastozoología, CONICET, Museo de La Plata, La Plata, Argentina

A. Itatí Olivares Sección Mastozoología, CONICET, Museo de La Plata, La Plata, Argentina

Bruce D. Patterson Negaunee Integrative Research Center, Field Museum of Natural History, Chicago, IL, USA

Cristian E. Schleich Grupo ‘Ecología Fisiológica y del Comportamiento’, Instituto de Investigaciones Marinas y Costeras, Universidad Nacional de Mar del Plata, Consejo Nacional de Investigaciones Científicas y Técnicas, Mar del Plata, Argentina

Pablo Teta División Mastozoología, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina

Aldo I. Vassallo Grupo Morfología Funcional y Comportamiento, Instituto de Investigaciones Marinas y Costeras (IIMyC, UNMDP-CONICET), Universidad Nacional de Mar del Plata (UNMdP), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Mar del Plata, Buenos Aires, Argentina

Diego H. Verzi Sección Mastozoología, CONICET, Museo de La Plata, La Plata, Argentina

Roxana R. Zenuto Grupo 'Ecología Fisiológica y del Comportamiento', Instituto de Investigaciones Marinas y Costeras, Universidad Nacional de Mar del Plata, Consejo Nacional de Investigaciones Científicas y Técnicas, Mar del Plata, Argentina

About the Editors

Thales Renato Ochotorena de Freitas has been a full professor in the Department of Genetics, Institute of Biosciences, Federal University of Rio Grande do Sul (UFRGS), since 1985. He earned his Ph.D. in genetics and molecular biology (1990) from UFRGS. He has been a visiting scholar at the Museum of Vertebrate Zoology, University of California-Berkeley (1996–1997), and visiting researcher at Laboratoire d'Écologie Alpine, University of Grenoble (2013–2014), where he worked on cutting-edge genomic tools. Dr. Freitas is currently investigating variation at population and species levels in *Ctenomys*, particularly from groups on the border of the Amazon Forest and coastal plain, using cytogenetic and molecular genetics. Dr. Freitas serves as director of the Graduate Program in Genetics and Molecular Biology at UFRGS and was the founder president of the Brazilian Society of Mastozoology (SBMZ). He teaches classical genetics and conservation genetics to undergraduate and graduate students.

Gislene Lopes Gonçalves has been a research collaborator in the Department of Genetics, Federal University of Rio Grande do Sul (UFRGS), Brazil, and at the Universidad de Tarapacá, Chile, since 2014. She earned her Ph.D. in genetics and molecular biology (2011) from UFRGS, where she completed her postdoctoral studies in zoology (2012–2016). She has been a visiting researcher at the Museum of Comparative Zoology, Harvard University (2009–2010), where she worked on the genetic basis of hair pigmentation in rodents with Professor Hopi Hoekstra. Dr. Gonçalves is currently interested in editorial works and collaborates with numerous research groups in the scope of evolutionary genetics.

Renan Maestri has been an assistant professor in the Department of Ecology, Institute of Biosciences, Federal University of Rio Grande do Sul (UFRGS), since 2018. He is also a research associate at The Field Museum of Natural History, Chicago, IL, USA, since 2020. He earned his Ph.D. in ecology (2017) from UFRGS, with a period in The Field Museum, and completed his postdoctoral studies in the Graduate Program in Animal Biology (2017–2018), UFRGS. Dr. Maestri teaches and advises students in the field of ecology and evolution, and coordinates the

Laboratory of Ecomorphology and Macroevolution at the Department of Ecology, UFRGS. He is interested in the areas of evolutionary biology, ecology, and biogeography, with an emphasis on morphological evolution, macroevolution, and macroecology of complex phenotypes.

Part I
Evolution of *Ctenomys*

Chapter 1

The History of *Ctenomys* in the Fossil Record: A Young Radiation of an Ancient Family



Diego H. Verzi, Nahuel A. De Santi, A. Itatí Olivares, Cecilia C. Morgan, and Alicia Álvarez

1.1 Introduction

Ctenomyidae is a clade of South American hystricomorph rodents with a peculiar evolutionary history characterized by: strong morphological differentiation, i.e., modernization that took place in the late Miocene; extinction of lineages during the Plio-Pleistocene, which led to *Ctenomys* being the only representative of the clade in the living fauna; and an extremely high rate of speciation of the latter genus, which is unmatched among caviomorphs (Reig et al. 1990; Lessa et al. 2008; Verzi 2008; Verzi et al. 2014, 2016; Álvarez et al. 2017, 2020). The stage of morphological differentiation is defined by the acquisition of a unique dental morphology, which persists in living species (Reig 1970). Because of its uniqueness, the appearance of this dental morphology has dictated the recognition of ctenomyids in the fossil record (Wood 1955; Reig et al. 1990; Arnal and Vucetich 2015). In addition, the skeletal morphology of modern ctenomyids diversified in adjustment to life underground. Because of their unequivocal recognition, as well as their appealing adaptive diversification, these modern representatives have attracted the attention of paleontologists almost exclusively; the corpus of information produced, primarily systematic and paleobiological, has provided knowledge on the boundaries of specialization explored by at least part of the clade throughout its history (Reig and Quintana 1992; Casinos et al. 1993; Quintana 1994; Fernández et al. 2000; Vieytes et al. 2007; Lessa et al. 2008; Verzi 2008; Morgan and Verzi 2011).

With regard to the other major contribution of fossils, i.e., the estimation of the time of origin and extinction of lineages and clades, this is an issue that remains still

D. H. Verzi (✉) · N. A. De Santi · A. I. Olivares · C. C. Morgan
Sección Mastozoología, CONICET, Museo de La Plata, La Plata, Argentina
e-mail: dverzi@fcnym.unlp.edu.ar; ndesanti@fcnym.unlp.edu.ar;
iolivares@fcnym.unlp.edu.ar; cmorgan@fcnym.unlp.edu.ar

A. Álvarez
Instituto de Ecoregiones Andinas, CONICET, Jujuy, Argentina

partially unresolved and unclear for ctenomyids. This stems not only from the need for more, and more exhaustive, phylogenetic analyses that include extinct species but also from the dissimilar current interpretations regarding the evolutionary meaning of these extinct taxa. Fossils provide estimations of the divergence times of clades as raw information, and subsequently through the calibration of molecular clocks (Benton and Donoghue 2007; Ronquist et al. 2016). Consequently, they play a central role in the analysis of evolutionary patterns, models, and rates. Nevertheless, reliable age estimations require hypotheses regarding the correspondence of fossils to the different evolutionary stages of a clade: origin, modernization, and establishment of the crown group (Hennig 1965). As previously mentioned, the paleontological studies of ctenomyids have been essentially focused on the modern species; however, in this context of analysis, these have little to contribute to the knowledge of the origin of the clade, or even, depending on their phylogenetic position, of the origin and diversification of the crown group. Thus, achieving an understanding of the evolutionary pattern of this family, including the times and rates of taxonomic and morphological diversification of living species (e.g., Álvarez et al. 2017; Caraballo and Rossi 2018), still requires a more accurate interpretation of the fossil record.

In this chapter, we offer a brief review of the history of the family Ctenomyidae such as it can be interpreted through its fossil record. In addition to describing major characteristics of this history, we provide a critical assessment of the potential contribution of available information to the estimation of divergence times through the phylogeny of the family, with emphasis on its single living representative, *Ctenomys*.

1.2 Stem Ctenomyids and the Understanding of Ctenomyid Origin

The family Ctenomyidae has been traditionally recognized by the rootless molars with exceptionally simplified occlusal surfaces that characterize its late Miocene to Recent representatives (Simpson 1945; Wood 1955; Reig et al. 1990; Vucetich et al. 1999; Arnal and Vucetich 2015). Alternatively, Verzi (1999) proposed an octodontoid with conservative rootless molars with lophids and flexids, the lower late Miocene †*Chasichimys*, as potential ancestor of the modern ctenomyids (see also Verzi et al. 2004a). Later phylogenetic analyses supported the position of †*Chasichimys*, the related †*Chasicomys* (late Miocene), and the older †*Sallamys* (late Oligocene), †*Willidewu*, and †*Protadelphomys* (early Miocene) as stem ctenomyids (Fig. 1.1; Verzi et al. 2014, 2016). However, this unorthodox phylogenetic hypothesis is far from consensus. With the exception of †*Chasicomys* (see Pascual 1967), these genera were initially assigned to Echimyidae (e.g., Simpson 1945; Wood 1955; Wood and Patterson 1959; Patterson and Pascual 1968; Patterson and Wood 1982; Vucetich and Verzi 1991), a family whose living representatives maintain rooted molars with conservative morphologies (Verzi et al. 2016, Fig. 1.1). Phylogenetic analyses based essentially on dental characters have supported the

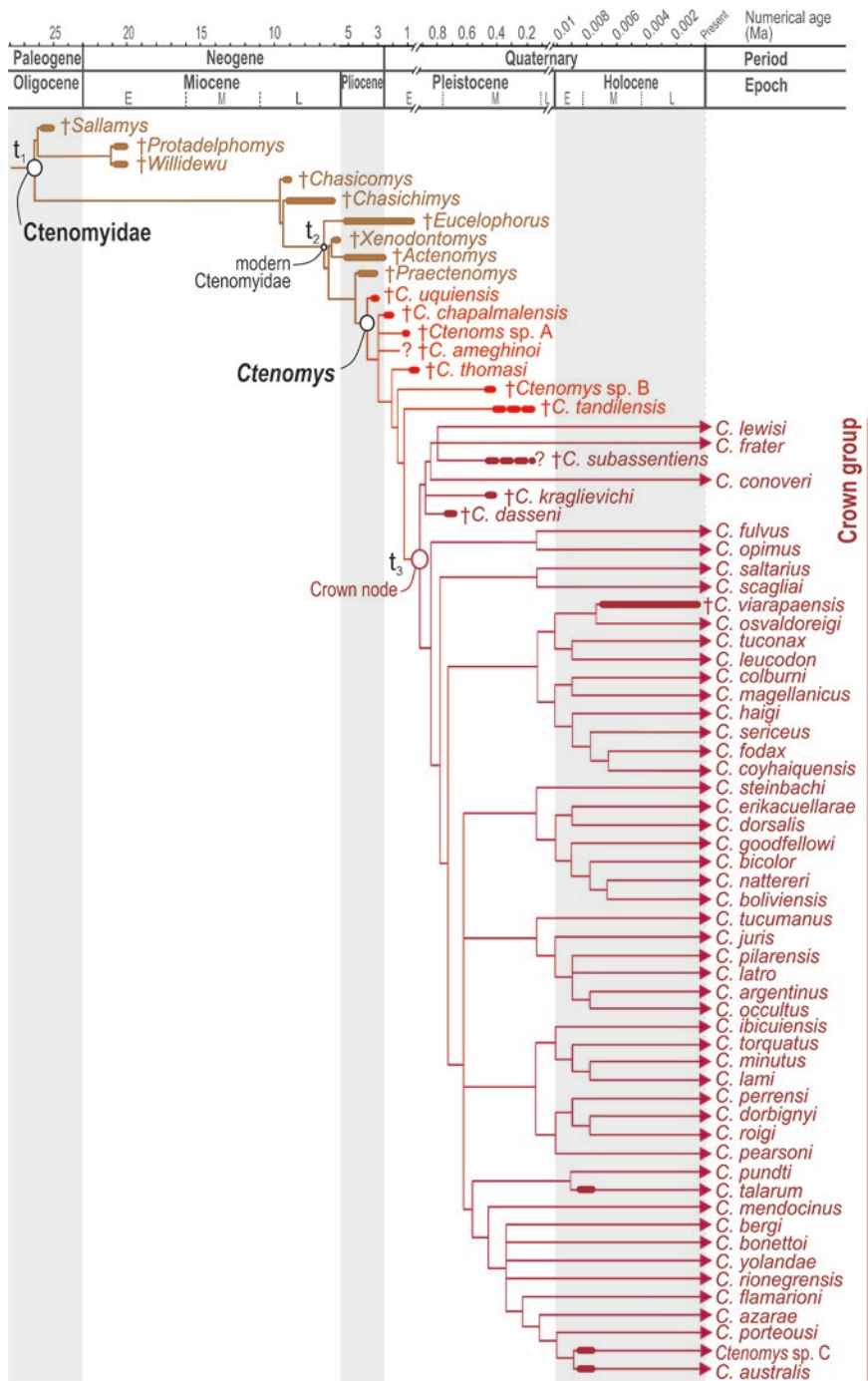


Fig. 1.1 Strict consensus of eight most parsimonious trees resulting from parsimony analysis of combined morphological and molecular data. Divergence times for species of the crown group is according to a Bayesian tip-dating analysis by De Santi et al. (unpubl. results)

inclusion of †*Protadelphomys* within Echimyidae and have recovered †*Sallamys* as a stem Octodontoidea (Carvalho and Salles 2004; Arnal and Vucetich 2015; Boivin et al. 2019).

These dissimilar results regarding the affinities of these early octodontoids are due, at least in part, to different interpretations of dental characters for different species samplings, an issue that still needs critical revision. In a recent meta-analysis of phylogenetic reconstructions, Sansom et al. (2017) showed that dental data are generally less reliable than osteological data as indicators of phylogenetic history. In this sense, the preserved cranial remains of †*Protadelphomys* possess at least two informative traits in the orbital and auditory regions that are shared with modern and living ctenomyids; in addition, this genus does not share with the Echimyidae any key synapomorphies of the auditory region that are diagnostic of this latter family (Verzi et al. 2014, Fig. 6; Verzi et al. 2016, Fig. 9).

In any case, even when accepting †*Sallamys*, †*Protadelphomys*, and †*Willidewu* as stem ctenomyids, their phylogenetic position is less strongly supported than that of the late Miocene-Pleistocene modern representatives (see Verzi et al. 2014). In this sense, the abovementioned and best-known concept of Ctenomyidae, restricted to the species with rootless simplified molars, is undoubtedly more stable. This concept of Ctenomyidae represents an apomorphy-based clade, defined by the acquisition of rootless crescent-shaped molars that took place in the late Miocene (Figs. 1.1 and 1.2). Such apomorphy-based clade comprises late Miocene to

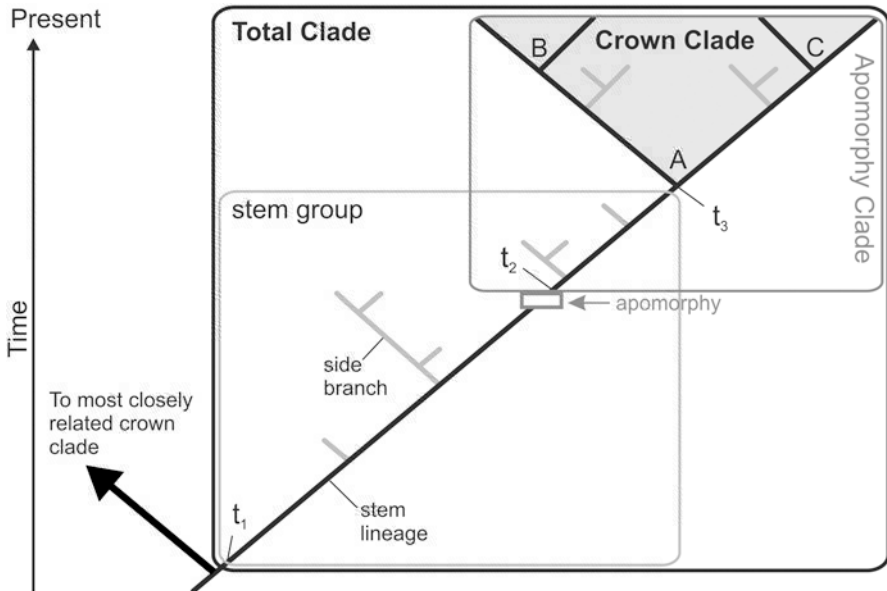


Fig. 1.2 Chart showing categories of clades and related concepts after de Queiroz (2007, Fig. 1.2). Grey branches represent lineages lacking extant descendants (side branches); black branches represent lineages with extant descendants. The apomorphy clade is represented as corresponding to stage t2 by assuming that the marked apomorphy is that which defines the beginning of this stage

Pleistocene stem representatives and the living *Ctenomys* (Fig. 1.1). Differentiation of lineages and genera among these modern ctenomyids would have resulted from the acquisition of disparate adaptations to digging and life underground (Reig and Quintana 1992). Four cohesive lineages are recognized: †*Eucelophorus* (early Pliocene-middle Pleistocene), †*Xenodontomys*-†*Actenomys* (late Miocene-late Pliocene), †*Praectenomys* (Pliocene), and †*Ctenomys* (late Pliocene-Recent). The †*Xenodontomys*-†*Actenomys* lineage would have had fossorial habits, while *Ctenomys* and †*Eucelophorus* independently acquired craniodental specializations for subterranean life (definition of fossorial and subterranean habits follows Lessa et al. 2008); †*Praectenomys* would have been at least fossorial (Verzi 2008; Verzi et al. 2010).

Beyond their different support or stability, the previously mentioned alternative definitions of Ctenomyidae are conceptually different and represent different times of the history of the clade. Three successive stages can be recognized in the evolutionary history of any clade with living representatives, referred to as t1, t2, and t3 by Hennig (1965: Fig. 1.4): t1, the time of its origin by divergence from the most closely related clade with living representatives; t2, its time of morphological differentiation or modernization by the acquisition of the apomorphy or apomorphies that characterize its extant members; and t3, the time of the origin of the last common ancestor of the living representatives. The nested clades that result from each of these points of origin are defined as a total clade, apomorphy clade, and crown clade, respectively (Fig. 1.2; de Queiroz 2007). A total clade comprises the crown clade and its corresponding stem group. The stem group is by definition paraphyletic and includes both extinct species that are directly ancestral to the crown, i.e., those belonging to the stem lineage, and those that are not directly ancestral, i.e., side branches.

In this context, modern ctenomyids with derived molars represent Hennig's stage t2 (Fig. 1.1). Hennig (1965: 114) pointed out that the delimitation of the stage of morphological differentiation, t2, depends on subjective criteria concerning the interpretation of the emergence of particular "types" or "Baupläne". We consider that this stage is related to change within lineages, and although its delimitation may imply subjectivity, it can yield important evolutionary information on environmentally-driven morphological changes (Verzi et al. 2014, 2015). Beyond this, even though many of the fossils at this stage of morphological differentiation may be stem representatives, as occurs in ctenomyids (Fig. 1.1), they do not provide relevant contributions to the interpretation of the origin of the total clade within which they are nested. The practice of interpreting the origin of clades from the first appearances of the main diagnostic characters shared with extant representatives should be assumed as an operational restriction. As pointed out by de Queiroz (2007: 968), the origins of total clades have to do with lineage splitting rather than with character state transformations. Consequently, for an apomorphy to be present in the earliest members of a total clade, that apomorphy would have to have arisen and become fixed simultaneously with the lineage-splitting event in which the clade originated. Because of the nature of evolutionary processes and hierarchies involved in that lineage-splitting event, the latter is not to be expected. As a result, early stem

members share few “non-key” apomorphies with their corresponding crown-group (Steiper and Young 2008). In any case, the difficulty of separating the earliest representatives of two diverging extant clades does not negate the validity of the splitting point as the origin of the resulting clades (Briggs and Fortey 2005: 100). Thus, efforts focused on the recognition of plesiomorphic early stem lineages and side branches are indispensable to interpret the deep history of a surviving clade.

Here we lend more support to the idea of applying the name Ctenomyidae to the total clade (see below). †*Sallamys*, recorded in the late Oligocene of Bolivia and Peru, is its earliest stem representative (Fig. 1.1; Patterson and Wood 1982; Shockey et al. 2009). Recently, Pérez et al. (2019) transferred the species †*Sallamys quispea* from the late Oligocene of Peru to the genus †*Migraveramus*; we consider that the molar morphology of †*S. quispea* is comparable to that of the type species †*Sallamys pascuali* albeit less abbreviated (Shockey et al. 2009, Fig. 6), and therefore suggest that the former species should remain to be assigned to †*Sallamys*.

The proposals of paleontological ages younger than 10 My for this family (e.g., Reig 1989; Reig et al. 1990; Vucetich et al. 1999; Arnal and Vucetich 2015; Vucetich et al. 2015) should be reinterpreted as associated to the beginning of the modernization stage, t2 (Fig. 1.1). According to biochronological data, the earliest species corresponding to this stage, †*Xenodontomys simpsoni*, is approximately 6 My old.

1.3 The Genus *Ctenomys*

Information on the early history of the lineage that leads to *Ctenomys* is fragmentary and unclear. The available data hinder a temporal assignment more precise than the entire Pliocene for the divergence of this lineage from the sister genus †*Praectenomys* (see review of the age of Umala Formation in Cione and Tonni 1996). An unpublished mandibular fragment affine to *Ctenomys*, but with only a slight reduction of m3, was recently found in the early Pliocene of western Argentina (Verzi unpublished). Although no phylogenetic analyses have yet been made, this new fossil would represent an intermediate step in the acquisition of the apomorphies that characterize the *Ctenomys* lineage, being closer to the latter than to the one currently considered as sister genus, †*Praectenomys*.

Thus, while *Ctenomys* is a morphologically cohesive genus in the living fauna (Reig et al. 1990; Vassallo and Mora 2007), its boundaries become less evident when the variation of the oldest related extinct species is considered. By application of an adaptation-rooted criterion, which involves an assessment of both the monophyly and the adaptive profiles to delimit genera in the fossil record (Wood and Collard 1999; Cela-Conde and Ayala 2003), the species †*Ctenomys uquiensis* (late Pliocene) and †*Paractenomys chapalmalensis* (lower early Pleistocene) have been considered as the earliest members of the genus *Ctenomys* (Fig. 1.3; Verzi 2008; Verzi et al. 2010). Although part of their traits are undoubtedly plesiomorphic with respect to living species (Verzi 2002; Morgan and Verzi 2006, 2011), functionally significant specializations and the conserved allometry of their masseteric

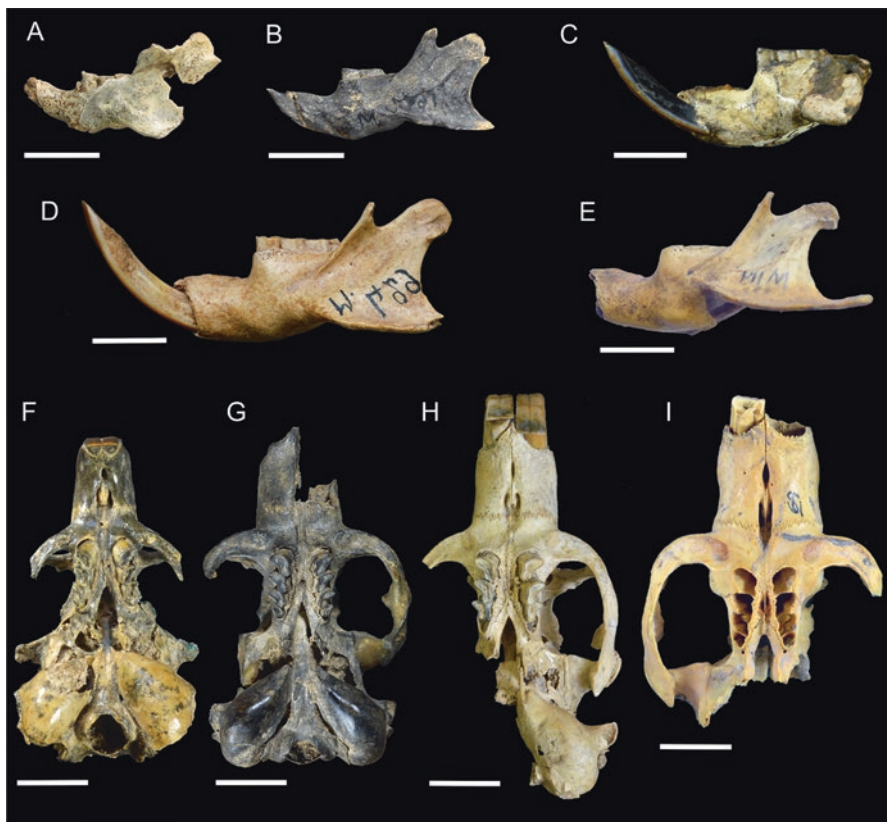


Fig. 1.3 Mandibles and skulls of some extinct species of *Ctenomys* mentioned in the text. Left mandible of: (a) †*C. uquiensis* MLP 96-II-29-1 (holotype); (b) †*C. chapalmalensis* MMP 1622-M (right reversed); (c) †*C. dasseni* PVL 739 (holotype); (d) †*C. kraglievichi* MMP M-429 (right reversed); (e) †*C. viarapaensis* MLP 2966. Ventral view of skull of: (f) †*C. chapalmalensis* MMP 481-S; (g) †*C. dasseni* (holotype of †*C. intermedius* MACN 1849); (h) †*C. kraglievichi* MSC MS 20-1; (i) †*C. viarapaensis* MLP 2935 (holotype). MACN, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; MLP, Museo de La Plata, Argentina; MMP, Museo de Ciencias Naturales de Mar del Plata, Argentina; MSC, Museo de Ciencias Naturales de Santa Clara, Argentina; PVL: Colección Paleontología Vertebrados, Instituto Miguel Lillo, San Miguel de Tucumán, Argentina

morphology, in the comparative context of the modern ctenomyids, support the inclusion of these species within the genus (Verzi 2008; Verzi et al. 2010).

The genus *Ctenomys* thus delimited represents an apomorphy clade with a minimum age, given by †*C. uquiensis*, close to 3.5 My (Fig. 1.1). However, given that these species are ancestral to the crown clade (Verzi 2008; Verzi et al. 2010; De Santi et al. 2020), this estimation marks a maximum constraint (softbound) on the age of the crown (Benton and Donoghue 2007). Ongoing phylogenetic analyses (De Santi et al. 2020; unpublished results) that include the most complete fossil materials of extinct species accepted as valid suggest that the crown clade *Ctenomys* is