Natural and Social Sciences of Patagonia

Mariana Morando
Luciano J. Avila
Editors

Lizards of Patagonia

Diversity, Systematics, Biogeography and Biology of the Reptiles at the End of the World

Springer

Natural and Social Sciences of Patagonia

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Despite being an underpopulated region, Patagonia has attracted the attention of scientists since the very beginning of its settlement. From classical explorers such as Darwin or D'Orbigny, to modern science including nuclear and satellite developments, several disciplines have focused their efforts on unraveling Patagonia's natural and social history. Today, scientific and technological research is shifting from being shaped by northern agendas, towards more locally oriented objectives, such as the management of natural resources, the modernization of energy production and distribution, and the coexistence of rural and cosmopolitan social lifestyles. At the intersection of all these topics, new conflicts concerning the economy, human development, population, and the proper and long-standing planification and management of the landscape and its natural resources have emerged. These conflicts, of course, have also caught the attention of many interdisciplinary research groups.

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Editors
Mariana Morando
Instituto Patagónico para el Estudio de los Ecosistemas Continentales
Consejo Nacional de Investigaciones Científicas y Técnicas
Puerto Madryn, Chubut, Argentina

Luciano J. Avila
Instituto Patagónico para el Estudio de los Ecosistemas Continentales
Consejo Nacional de Investigaciones Científicas y Técnicas
Puerto Madryn, Chubut, Argentina

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For our parents
For our son
For all our teachers who made a difference
in our lives

Foreword

My introduction to Patagonia began with an email I received in 1999 from a young woman named Mariana Morando, doing research at a small field station in the tiny town of Anillaco (300 residents), in the Argentinian Province of La Rioja. She briefly explained to me that she was planning to conduct dissertation research on chromosome evolution in a group of Andean lizards in the genus *Liolaemus*. She had seen some of my earlier studies on chromosome evolution and "speciation potential" in the *Sceloporus grammicus* complex of Mexico and was interested in perhaps moving in this direction with *Liolaemus*. Both genera are characterized by interspecific variation in diploid numbers; in the genus *Sceloporus*, these range from $2n = 22$ to 46, and within the *S. grammicus* complex (2–3 species), $2n = 32$ to 46. In my sampling across the Mexican Plateau, I had studied two hybrid zones, one in great detail ($3n = 34 \times 46$) to test hypotheses about the role chromosomal rearrangements might play in driving speciation. In good English, Mariana indicated an interest in these themes and wanted to know if I could accommodate her and her husband Luciano, for one year if they could secure some financial aid.

At this time, I had four PhD students and two full-time post-docs in my lab; I was not really excited about trying to accommodate two more people, especially those I had never met. Further, I knew little about Argentina, but given my long-running research program on various groups of *Sceloporus*, I was vaguely aware that the genus *Liolaemus* might be a possible southern hemisphere analog. I was familiar with the *Liolaemus* cytogenetics studies on the chromosome races in the *L. monticola* complex described by Prof. Madeleine Lamborot (Univ. de Chile—Santiago) and noted some similarities between those lizards and the *S. grammicus* complex. I thought that some further work on this South American genus would be a good investment, so I replied to Mariana to ask for additional information from both of them. She replied that she was interacting with BYU MS graduate student Julie Tolman, who was working on lizard behavior and ecology at the Anillaco field station. Julie had passed on to Mariana & Luciano details about BYU and my lab, which Mariana and Luciano later told me were invaluable to them.

We sorted everything out, and Mariana Morando and Dr. Luciano Avila landed in Salt Lake City on 22 August 2000. I met them at the airport, drove them to Provo, checked them into a rental place, and then with my wife Joanne took them to a small informal "social" that evening with the people in my lab. Mariana was animated, while Luciano was more reserved, in part because his command of English was not as good, but he is also an introvert (as am I).

I do not remember all of the details, but both of them had personal savings and some funding for one year, and by various means through Argentina, BYU, and the US National Science Foundation, we secured support for another 2.5 years. Mariana quickly picked up the DNA sequencing protocols, scoring of gels, and organizing and analyzing data. We had recently hired Dr. Keith Crandall in a population genetics position, and he was proving to be "golden" with everything he touched. His academic credentials were stellar: PhD with Alan Templeton at Washington University, followed by a post-doc at the University of Texas-Austin with David Hillis. Keith "hit the ground running" at BYU; he supported Spanish PhD David Posada, and the two of them developed a computer program to implement a novel population genetics algorithm known as Nested-clade Analysis. With this software, Mariana, Luciano, and I completed some very nice manuscripts published in top tier journals (*Evolution*, *Systematic Biology*). Mariana's passion focused on conceptual issues in evolutionary biology, while Luciano was more of a "classical" systematist/taxonomist; he spent a lot of time collecting morphological data, but also picked up the DNA technologies, relevant analytical methods, and was first author on these same kinds of manuscripts. I was able to join them on my first trip to Argentina, then later a second trip, and their son Tadeo Ivan Avila was born in Provo in November 2003. Time passed quickly and after ~3.5 amazingly productive years, the three of them returned to Argentina in February 2004. This began a collaboration that continues to this day.

My first field trip to Argentina was with the two of them; we left Utah on 13 January 2003, arrived and got things organized in Río Cuarto, and departed with two others for fieldwork over a large part of Argentina. In checking my field notes, I find the following total species diversity for the ~2 weeks of fieldwork, as listed in my field catalog: *Leiosaurus* sp., *Cnemidophorus* sp., *Teius teyou*, *Homonota fasciata*, 2 recognized and one undescribed species of *Phymaturus* (*P. palluma*, *P. patagonicus*, and *P.* sp.), 16 recognized species of *Liolaemus* (*austromendocinus*, *bibronii*, *buergeri*, *chacoensis*, *cuyanus*, *darwinii*, *donosobarrosi*, *elongatus*, *fitzingeri*, *gracilis*, *goetschi*, *grosseorum*, *petrophilus*, *saxatilis*, and *wiegmannii*), and also: *L.* sp. nov., *L.* sp. "*buergeri*," *L.* sp. "*elongatus*," *L.* "*melanops*," *L.* cf. "*rothi*," and two *L.* sp. "cf *darwinii*." I also noted at a remote campsite in southern Mendoza Province, on the Payún Plateau, we collected 8 species of lizards within an area of probably less than two hectares of structurally very simplified habitat. These included: *Homonota darwinii, Leiosaurus belli, Liolaemus austromendocinus*, *L. darwinii*, *L donosobarrosi*, *L. gracilis*, *L. grosseorum*, and *L. parthenos*. To the best of my knowledge, this level of "species packing" was unheard of! These lizards varied in body size, but this alone seemed inadequate to explain how so many species could live in what to us looked like a very simplified environment. I am not an ecologist, but I have mentioned this observation to *Anolis* researcher Jon Losos, and he had no explanation either. As I was learning, *Liolaemus* and its smaller sister genus *Phymaturus* offer a lot of intellectual "low hanging fruit"; a multitude of interesting taxonomic and phylogenetic questions waiting for study, which will lead to more "low hanging fruit" for ecological studies.

In March 2007, I participated in my first field trip into Chilean Patagonia, organized by colleagues Pedro Victoriano (U. Concepcion) and Jose J. Nuñez ("Pepe"; U. Austral, Valdivia), who study lizards and frogs, respectively. We packed and headed south from Valdivia on 5 March 2007, and on these wetter western slopes of the Andean Cordillera we traveled through forest habitats. Much of the land was cleared for agriculture, but that decreased and forest cover increased as we headed further south. This side of Patagonia is much narrower than the arid Argentinian side, and the steep altitudinal gradient from the Pacific Coast to the high Chilean Peaks wrings most of the moisture from the clouds before they pass over the high ranges into Argentina. Biologically, this wetter climate translates into reduced lizard species richness, but frog diversity is much higher and was therefore included in our research program here. We operated here the same way as in Argentina and collected lizards under bark on fallen trees on rainy days, or basking on sunny days. Over the next 16 days, we collected five lizard species: *Liolaemus chiliensis, L. cyanogaster, L. lemniscatus, L. pictus,* and *L. tenuis*, and seven genera of frogs representing four families. As in Argentina, the lizard species were distributed over wide geographic areas with extensive variation in elevation and ecological conditions; phylogeographic studies showed that some of these were likely to contain "candidate species". It was also obvious that while these temperate rainforests harbored fewer lizards, anuran biodiversity appeared to be higher. This was indeed the case, and Pepe has since described frog species from this region.

I visited both countries again, hosted these investigators and their students at BYU, and am fortunate to have spent so much professional and social time with such great colleagues. I was delighted to be asked to write the preface for this book. My personal experience in this part of the world includes the modest fieldwork noted above, and my research collaborations include only a small number of Patagonian scholars, focused only on two groups of vertebrates. However, reading the 14 chapters of text, I realized that this preface would be an ideal way to let the rest of the academic world know about this remarkable book.

The book is entitled: "Lizards of Patagonia: Diversity, Systematics, Biogeography, and Biology of the Reptiles at the End of the World," and it treats us to an introduction and thorough overview of the lizard fauna in this fascinating region. Chapters 1–6 cover "History of Discovery," "The Relationship Between People and Lizards in Patagonia," "Landscapes and Geology of Patagonia, and Introduction to the Land of Reptiles," "Geographical Singularities of the Patagonian Climate," "Vegetation of Patagonia," and "The Patagonian Fossil Lizards." These sections provide a thorough background in which past and ongoing taxonomic, systematic, and ecological studies have taken place. These include "Naming the Diversity: Taxonomy of Current Species of Patagonian Lizards," "Biogeography, Ecology, and Spatial Patterns of Patagonian Lizards," "Diversification and Evolutionary Histories of Patagonian Steppe Lizards," "Biogeography, Ecology, and Spatial Patterns of Patagonian Lizards," "Phylogeography of Chilean Lizards: Histories of Genetic

Diversification on the Western Slope of Austral Andes," "General ecology of Patagonian Lizards," "Reproductive Biology of Lizards from Cold and Harsh Environments of Patagonia Argentina," "Effects of Global Warming on Ecophysiology of Lizards of Patagonia, Argentina," and "Conservation of Lizards from Patagonia: Current Status, Trends, and Management Proposals." Leading researchers have done a superb job at summarizing the histories and current states of knowledge of their respective disciplines, and the editors are to be congratulated for their efforts in pulling all of this together in a single book. It deserves a wide readership.

Brigham Young University
Provo, UT, USA

Jack W. Sites, Jr.

Preface

As a young child, Luciano Avila was curious about animals, over the years he kept a collection of species that neighbors would find lost in their crop-fields. At that time, the travels and adventures of Jacques Yves Cousteau or Félix Rodríguez de la Fuente, famous documentarians, stimulated most of the biology students. In 1984, when he was an undergraduate at the small Universidad Nacional de Río Cuarto, thanks to Juan Carlos Acosta (one of the coauthors of Chap. 11), he was invited to a short biologists' field trip to La Helvecia, a lagoon in southern Córdoba Province, that at that time had an extraordinary fauna; Luciano's group "fell in love" with birds. The next year, they asked one of the few vertebrate professors, Dr. Ricardo (*Richard*) Martori, if he could advise them on how to do an honor's thesis on birds, but Dr. Martori proposed lizards as a better choice. Almost by accident then, Luciano became interested in Herpetology. They learned that Richard had worked many years in the Córdoba serpentarium and was fond of reptiles. Somehow disappointed, they had to leave birds out of the picture, they accepted his proposal because he was a nice person and above all they wanted to work with him. Luciano started working with the lizard genus *Teius*, and very quickly, his interest in lizards grew, partly as a result of the many field trips he participated in. One of these trips took his group to a small mountain range ~90 km from Río Cuarto, and together with JC Acosta, they collected lizards they could not identify with Cei's 1986 book. Juan Carlos Acosta suggested that this lizard may be a new species, but Luciano was at first very skeptical; he could not imagine that an undescribed species might be found one hour away from the university. Prof. Martori suggested that the students consult Jose Miguel Cei himself, at that time Honorary Professor at Universidad Nacional de Río Cuarto. Dr. Cei made regular visits to the University, as he at that time worked with another professor on amphibians. Luciano showed the lizards to Cei on his next visit, and with an excited mix of Italian and "Argentinean Spanish," Cei exclaimed: "eh! Luciano, this is a new species!" Then, next season with more individuals collected they described *Liolaemus saxatilis*.

Cei told Luciano about unknown places and almost "mysterious" species from the Andes and Patagonia, increasing his enthusiasm, soon Cei's book became "the book" for Luciano. Searching for a doctoral thesis was a huge challenge in Argentina at that time. The country was immersed in an acute economic crisis (sadly, this now seems to be the norm here…), and there were fewer than five herpetologists in the country who could act as advisors. Luciano continued his studies on *Teius*, with Gustavo Scrocchi (a young CONICET researcher) and Ricardo Martori as advisors, in the PhD program at Universidad Nacional de Tucumán. This allowed him access to the Fundación Miguel Lillo Herpetological collection, which included the largest collections of *Liolaemus* in the world, all carefully stored in closed cabinets. This only increased the mystery about these lizards for Luciano and while at Tucumán, Luciano also met the famous herpetologist Dr. Raymond Laurent. Also, as luck would have it, the son of a UNRC professor, Sergio Tiranti brought Luciano more lizards that again he could not identify with Cei's book. Cei himself was not able to precisely identify these lizards, and they were eventually described as *Liolaemus mapuche*. Now highly motivated, in 1993 Luciano decided to go in search of these mysterious lizards; he took a bus for a long ride to northern Patagonia to a place called Cerro Bandera, in Neuquén Province. Upon arrival, he noticed that there were no traces of civilization, and his request to camp at an oil field was promptly denied. Of course, with a big beard, strange clothes, and a heavy backpack, the "I am looking for lizards" speech was not very convincing.

Undaunted, Luciano trekked alone through the "middle of nowhere" for 2 days, and he collected many individuals from various sizes and colors; his "confusion was very clear"—the extraordinary morphological and color variation in these lizards was huge and… well, it still is! Luciano's intention of finding an easy way to describe new *Liolaemus* species quickly disappeared as soon as he went back to the lab. From Cei's book, it was impossible to identify even what main species group these lizards might belong to. For now, this would all have to wait; finishing the *Teius* PhD thesis was his priority. At this time, Luciano was also the representative of the Argentine Environmental Olympiads at Río Cuarto, that allowed him to meet an environmental manager CEO of one of the oil companies stationed south of Cerro Bandera; this was the turning point that gave Luciano access to the oil fields, and his discovery of one of the most extraordinary new species that he later described as *Liolaemus gununakuna*. This species would without doubt qualify as one of the most beautiful of the genus. Cei made one last visit with Luciano and was not so excited with this new species, as the brilliant colors were lost in the preserved specimens, and they resembled another known species.

This did not matter to Luciano; his heart was now devoted to the Patagonian lizard fauna. He wondered that, after so many surprises on his single visit to Cerro Bandera, what discoveries awaited in the rest of all Patagonia and the Andean Cordillera? His PhD fellowship was ending, and with it all of these dreams as there were no academic options in Argentina at that time. Then the unexpected happened, CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas, main research institution in Argentina) decided to offer postdoctoral fellowships, and he secured one to conduct a systematic review on a local species from the Pampa region, *Liolaemus wiegmannii*. There was no support at this time for travel to distant localities. Eventually, CONICET offered a few permanent academic positions, and Luciano got his chance to become a researcher on Patagonian lizard diversity; his dream was becoming true. However, his position was in a new research center in Northern Argentina (those "logical" things that happen in Argentina). This was 1998 and at that time, Mariana Morando was searching for an opportunity to do a PhD research on her "love" since her teen years: genetics. Luciano lured her to join him in a small town (300 inhabitants) in the Argentinian "far west." The lab was literally completely empty (yes, just walls), but voilá—the region was also full of amazing *Liolaemus* lizards.

Mariana was accepted as a PhD candidate at Universidad Nacional de Tucumán, with Dr. G. Scrocchi as her advisor. She had to develop her project and the only affordable genetics option that could be supported with personal pocket money was cytogenetics. To collect Patagonian lizards, Luciano and Mariana secured credit, bought a small 3-doors car and headed to northern Patagonia. Although Mariana was forced by necessity to develop a cytogenetics theme, in her mind genetics was something else ("crazy sequencing stuff to discover how evolution works"). In her literature search, she found a paper by Dr. Jack Sites on *Sceloporus* cytogenetics that interpreted in an evolutionary context an otherwise descriptive pattern. She wrote an email asking for an opportunity to do an internship at his lab at Brigham Young University, in Provo, Utah, USA. Dr Sites was overwhelmed with PhD students but curious about this proposal and remembered that a MS student from his department had done fieldwork in Argentina recently, and serendipity happened. In this same tiny town lost in Northern Argentina, the BYU student had met Luciano and Mariana, and she gave nice enough credentials that Dr. Sites answered kindly to Mariana's email. Alas, he was entering the sequencing era and at that point this was a "dream come true" for Mariana; this began the story of a long-term fruitful collaboration, and a deep friendship now going on two decades. Mariana and Luciano used their savings to buy a limited number of cryo-tubes and headed to Patagonia again in their tiny car in search for lizards and began collecting tissues. They then bought plane tickets to the USA and invested all they had to go for a different kind of adventure: sophisticated lab techniques and newer conceptual approaches to phylogeographic and phylogenetic statistical analyses and species delimitation issues. One good thing brought another, Mariana was encouraged by David Posada and got generous financial help from Dr. Keith Crandall to stay in the USA as a student and earn a MS degree at BYU. Then several BYU faculty, with colleagues in Argentina and Chile, established an expanded collaborative network that secured them a National Science Foundation grant. In 2004, Mariana, Luciano, and their American-born son Tadeo moved back to Argentina, this time to a research institute in Puerto Madryn and a different new chapter began. They were finally living in Patagonia, and every field trip yielded new pieces of evidence about the evolutionary history of the Patagonian lizard fauna. The challenges are all more scientifically exciting and continue to impact every aspect of their academic and personal lives. Of course, Patagonia was also a land of opportunities for other researchers; in this book, our intention was to include as many as possible, and although some could not participate for different reasons, we have made every effort to also reflect their contributions. The book is organized into three parts. Part I includes two chapters, Chap. 1 provides a brief introduction to the history of the herpetological studies and current research groups studying lizards in Patagonia, and Chap. 2 presents the cosmovision of lizards within the cultural and symbolic context of original people of Patagonia. Part II focuses on the climate, landscape, and vegetation of the region. Chapter 3 gives an overview of different aspects of the climate, Chap. 4 describes the geomorphological characteristics, and Chap. 5 describes all the different vegetation components. Part III provides updated information on lizards' paleontological knowledge (Chap. 6), current taxonomy (Chap. 7), distributional patterns in a biogeographic context (Chap. 8), diversification and evolutionary history in Argentinean Steppe (Chap. 9), phylogeographic patterns in Chile (Chap. 10), general ecology (Chap. 11), reproductive aspects (Chap. 12), climate change and ecophysiology (Chap. 13), and conservation (Chap. 14).

Luciano and Mariana want to heartily thank all the individuals who were part of or have been related to the Grupo de Herpetología Patagónica (especially to Cristian H.F. Perez), and all the authors of this book who accepted the effort required for this collective contribution. We are also grateful to Tadeo Avila for his support through the years, from spending toddler years on long summer field trips to presently helping his parents with English grammar in some of the chapters. We are also grateful for our parents' unconditional support. We especially thank João Pildevasser who, as Springer representative, contacted us and offered to publish this book on Patagonian lizards. Saveetha Balasundaram and Cathrine Selvaraj from Springer for their help in editorial aspects. Bringing the Patagonian lizard book to completion involved the support, encouragement, and assistance of a plethora of people, including our recent students, as well as colleagues, Fauna authorities, research center administrators, museum curators, graduated students, interns, staff and support people from our research institute. This book was greatly improved by the input from a range of external reviewers for each chapter and for the original book proposal. Several colleagues helped us in different ways: S. Apesteguía, G. Bernardello, M. Bianchini, R. Brandao, F. Breitman, M.V. Brizio, A. Camargo, G. Colli, F. Coronato, P. Escudero, O. Frumento, J. Genise, F. Glaw, N. Ibargüengoytia, M. Kozykariski, A. Labra Lillo, G.A. Lobos Villalobos, F. Méndez de la Cruz, C. Navas, H. Núñez, D. Paz Barreto, N. Pelegrin, F. Torres-Pérez, J. Troncoso-Palacios, J.A. Scolaro, and J.W. Sites, Jr. Our research programs benefited from major contributions in grants, fellowships and jobs from CONICET, as well as grants from ANPCyT and UNPSJB, but the biggest support came from the PIRE and Macrosystem Biology programs of NSF through Brigham Young University thanks to our friend and colleague Jack W. Sites Jr.

Puerto Madryn, Argentina

Mariana Morando
Luciano J. Avila

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Contributors

Juan Carlos Acosta Gabinete Diversidad y Biología de Vertebrados del Árido (DIBIOVA), Departamento de Biología, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de San Juan, San Juan, Argentina

Centro de Investigaciones de la Geósfera y la Biósfera (CIGEOBIO-CONICET) Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de San Juan, San Juan, Argentina

Juana Aigo Instituto de Diversidad y Evolución Austral – Consejo Nacional de Investigaciones Científicas y Técnicas (IDEAus – CONICET), Puerto Madryn, Chubut, Argentina

Adriana María Albino CONICET – Departamento de Biología, Universidad Nacional de Mar del Plata, Mar del Plata, Argentina

Luciano J. Avila Instituto Patagónico para el Estudio de los Ecosistemas Continentales – Consejo Nacional de Investigaciones Científicas y Técnicas (IPEEC-CONICET), Puerto Madryn, Chubut, Argentina

Mónica Beatriz Bertiller Instituto Patagónico para el Estudio de los Ecosistemas Continentales – Consejo Nacional de Investigaciones Científicas y Técnicas (IPEEC-CONICET), Puerto Madryn, Chubut, Argentina

Andrés Bilmes Instituto Patagónico de Geología y Paleontología – Consejo Nacional de Investigaciones Científicas y Técnicas (IPGP-CONICET), Puerto Madryn, Chubut, Argentina

Alejandro Jorge Bisigato Instituto Patagónico para el Estudio de los Ecosistemas Continentales – Consejo Nacional de Investigaciones Científicas y Técnicas (IPEEC-CONICET), Puerto Madryn, Chubut, Argentina

Graciela Blanco Gabinete Diversidad y Biología de Vertebrados del Árido (DIBIOVA), Departamento de Biología, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de San Juan, San Juan, Argentina

Centro de Investigaciones de la Geósfera y la Biósfera (CIGEOBIO-CONICET) Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de San Juan, San Juan, Argentina

Jorgelina M. Boretto Instituto de Investigaciones en Biodiversidad y Medioambiente, Consejo Nacional de Investigaciones Científicas y Técnicas (INIBIOMA, CONICET-Universidad Nacional del Comahue), San Carlos de Bariloche, Río Negro, Argentina

Pablo José Bouza Instituto Patagónico para el Estudio de los Ecosistemas Continentales – Consejo Nacional de Investigaciones Científicas y Técnicas (IPEEC-CONICET), Puerto Madryn, Chubut, Argentina

Facundo Cabezas-Cartes Instituto de Investigaciones en Biodiversidad y Medioambiente, Consejo Nacional de Investigaciones Científicas y Técnicas (INIBIOMA-CONICET), San Carlos de Bariloche, Río Negro, Argentina

Fernando Raúl Coronato Instituto Patagónico para el Estudio de los Ecosistemas Continentales – Consejo Nacional de Investigaciones Científicas y Técnicas (IPEEC-CONICET), Puerto Madryn, Chubut, Argentina

Diego Omar Di Pietro Sección Herpetología, División Zoología de Vertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata - CONICET, Buenos Aires, Argentina

Fernando Duran Instituto de Investigaciones en Biodiversidad y Medioambiente, Consejo Nacional de Investigaciones Científicas y Técnicas (INIBIOMA-CONICET), San Carlos de Bariloche, Río Negro, Argentina

Paula C. Escudero Instituto Patagónico para el Estudio de los Ecosistemas Continentales – Consejo Nacional de Investigaciones Científicas y Técnicas (IPEEC-CONICET), Puerto Madryn, Chubut, Argentina

Jimena B. Fernández Instituto de Investigaciones en Biodiversidad y Medioambiente, Consejo Nacional de Investigaciones Científicas y Técnicas (INIBIOMA-CONICET), San Carlos de Bariloche, Río Negro, Argentina

Rodrigo Gómez Alés Gabinete Diversidad y Biología de Vertebrados del Árido (DIBIOVA), Departamento de Biología, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de San Juan, San Juan, Argentina

Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Buenos Aires, Argentina

Andrea González Marín Instituto Patagónico para el Estudio de los Ecosistemas Continentales – Consejo Nacional de Investigaciones Científicas y Técnicas (IPEEC-CONICET), Puerto Madryn, Chubut, Argentina

Nora R. Ibargüengoytía Instituto de Investigaciones en Biodiversidad y Medioambiente, Consejo Nacional de Investigaciones Científicas y Técnicas (INIBIOMA-CONICET), San Carlos de Bariloche, Río Negro, Argentina

Federico Pablo Kacoliris Sección Herpetología, División Zoología de Vertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata - CONICET, Buenos Aires, Argentina

Camila Kass CONICET, Sección Herpetología, División Zoología Vertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Buenos Aires, Argentina

Universidad Nacional de Chilecito, Instituto de Ambiente de Montaña y Regiones Áridas (IAMRA), CONICET, La Rioja, Argentina

Erika Kubisch Instituto de Investigaciones en Biodiversidad y Medioambiente, Consejo Nacional de Investigaciones Científicas y Técnicas (INIBIOMA-CONICET), San Carlos de Bariloche, Río Negro, Argentina

Ana Ladio Instituto de Investigaciones en Biodiversidad y Medioambiente, Consejo Nacional de Investigaciones Científicas y Técnicas (INIBIOMA-CONICET), San Carlos de Bariloche, Río Negro, Argentina

Cintia Débora Medina Laboratorio de Genética Molecular – UAT, CCT-CONICET CENPAT, Puerto Madryn, Chubut, Argentina

Marlin S. Medina Centro de Investigación Esquel de Montaña y Estepa Patagónica, Consejo Nacional de Investigaciones Científicas y Técnicas (CIEMEP-CONICET), Universidad Nacional de la Patagonia San Juan Bosco, Esquel, Chubut, Argentina

Ignacio Minoli Instituto Patagónico para el Estudio de los Ecosistemas Continentales – Consejo Nacional de Investigaciones Científicas y Técnicas (IPEEC – CONICET), Puerto Madryn, Chubut, Argentina

Mariana Morando Instituto Patagónico para el Estudio de los Ecosistemas Continentales – Consejo, Nacional de Investigaciones Científicas y Técnicas (IPEEC-CONICET), Puerto Madryn, Chubut, Argentina

Cristian Hernán Fulvio Pérez UAT, CCT-CONICET CENPAT, Puerto Madryn, Chubut, Argentina

Carla Piantoni Physiology Department, Bioscience Institute, University of São Paulo, São Paulo, Brazil

Kevin Imanol Sánchez Instituto Patagónico para el Estudio de los Ecosistemas Continentales – Consejo Nacional de Investigaciones Científicas y Técnicas (IPEEC-CONICET), Puerto Madryn, Chubut, Argentina

Barry Sinervo Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, CA, USA

Jack W. Sites Jr Biology Department and Monte L. Bean Life Science Museum, Brigham Young University, Provo, UT, USA

Department of Biology, Austin Peay State University, Clarksville, TN, USA

Jaime Troncoso-Palacios Programa de Fisiología y Biofísica, Facultad de Medicina, Universidad de Chile, Santiago, Chile

Pedro F. Victoriano Laboratorio de Microevolución y Ecología de Vertebrados (MEV), Departamento de Zoología, Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, Concepción, Chile

Jorge D. Williams CONICET, Sección Herpetología, División Zoología Vertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Buenos Aires, Argentina

Part I
Historical and General Background

Chapter 1
History of Discovery of the Patagonian Lizards

Jorge D. Williams, Camila Kass, and Luciano J. Avila

Abstract Knowledge of the history is necessary to understand why things are today as they are. Argentinean and Chilean Patagonia have a very interesting story about the native fauna and its discovery. The main character of this story is an adventurer spirit wanting to increase knowledge by traveling to the “end of the world”, ignoring barriers only to search and see what is beyond. Many well-known naturalists have visited this land eager and willing to find new species never seen before, while others have made some amazing contributions while never setting one foot on Patagonian soil. In this chapter, we intend to summarize how Patagonian herpetofauna was discovered, described and studied over time. In addition, we want to mention important scientists, whose work led the way for the future researchers to come.

Keywords Patagonia · History · Herpetologists · Discoveries · Darwin · Laurent · Cei · Donoso Barros · Koslowsky · Lizards

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J. D. Williams (✉)
CONICET, Sección Herpetología, División Zoología Vertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Buenos Aires, Argentina
e-mail: williams@fcnym.unlp.edu.ar

C. Kass
CONICET, Sección Herpetología, División Zoología Vertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Buenos Aires, Argentina

Universidad Nacional de Chilecito, Instituto de Ambiente de Montaña y Regiones Áridas (IAMRA), CONICET, La Rioja, Argentina
e-mail: ckass@undec.edu.ar

L. J. Avila
Instituto Patagónico para el Estudio de los Ecosistemas Continentales – Consejo Nacional de Investigaciones Científicas y Técnicas (IPEEC-CONICET), Puerto Madryn, Chubut, Argentina
e-mail: avila@cenpat-conicet.gob.ar

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1.1 Introduction

The aim of this chapter is to give the reader an idea of how intricate and fascinating the history of the discovery of Patagonian lizards is. We intend to summarize 304 years of research in a few pages where we will name the most significant researchers and naturalists who made contributions related to herpetology, emphasizing their work with Patagonian lizards.

There is a very interesting quote of the renowned Argentinean paleontologist Rosendo Pascual (1961), given by the Spanish botanist Angel L. Cabrera (1943) in a conference, where he stated that every country in its evolution towards the conquest of its scientific independence goes through four stages. At the beginning, the country remains closed to scientists all over the world. Second, it is explored by foreign scientists, which would carry on observations and organize collections, which would be of great benefit to the country. Third, a true concern for scientific advance starts in the country and then the country itself tries to arise interest in foreign researchers, on the basis that the influence of their work, experience and teaching can awake the interest for natural science in this new territory. At last, the country is scientifically emancipated, it carries on its own national investigation and if it contacts foreign scientists, it is only because they are specialists the country lacks. We agreed that the first of these stages would correspond to the founding times of the different South American countries, in the case of Argentina and Chile to the previous and contemporary years of their independence from Spain. So far, the different ethnic groups that inhabited Patagonia apparently knew how to recognize many animal species, and even gave them names, but this is addressed in another chapter of this book (Chap. 2).

1.2 The Beginning

The first record of lizards from Chile dates back to 1714, before Linnaeus nomenclature system, when the French abbot Louis Éconches Feuillée listed the presence of a salamander. He named this animal “salamandre acquatique et noire” (black and aquatic salamander) but nowadays we know this was a mistake because what he found at the time was a larva of a Chilean frog.

Abbot Juan Ignacio Molina (Fig. 1.1a), who is considered the first Chilean scientist, was born in Talca, Chile, in 1740. Although he wrote about diverse topics such as botany, climatology, geology, mineralogy and physical geography, he made important contributions to Chilean zoology and herpetology. He was the first scientist to use the binomial nomenclature proposed by Linnaeus in 1731 (Ortiz 2008). Even though the work he made describing new species was important, he had a main problem: he did not recognize most of the lizard species as natives or locals because he considered Chilean species to be the same as European ones (Donoso-Barros 1966). The development of herpetology in Chile began with the *Saggio sulla*

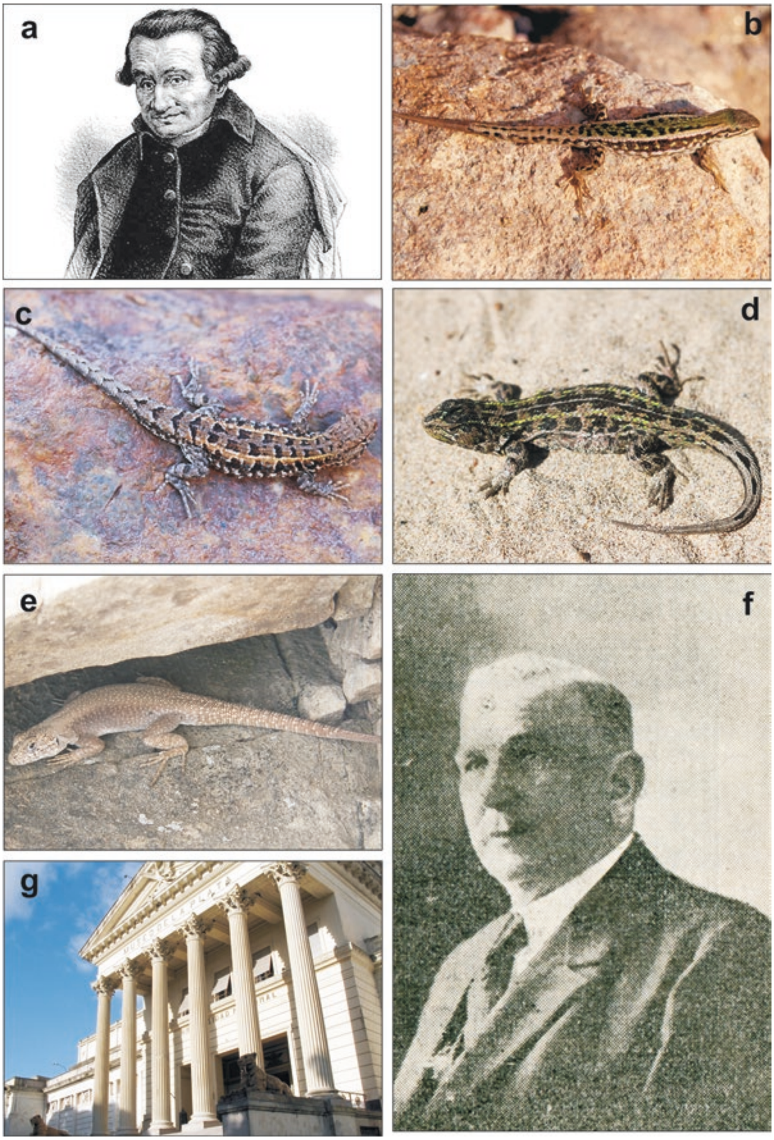


Fig. 1.1 (**a**) Drawing of abbot Juan Ignacio Molina (Courtesy A. Labra), (**b**) *Liolaemus chiliensis*, (**c**) *Liolaemus wiegmannii*, (**d**) *Liolaemus magellanicus*, (**e**) *Liolaemus burmeisteri*, (**f**) Julio Germán Koslowsky, (**g**) La Plata Museum frontispiece

storia naturale del Chile (Essay on the natural history of Chile) written by him in 1782 where he described one lizard and two amphibian species for Chile (Ortiz 2008).

1.3 The Nineteenth Century: The Age of Discovery

Eighty-three years later from Molina's work, in 1823, Coqueille's expedition brought René Primevère Lesson and Prosper Garnot, both surgeons and naturalists from France, who wrote *Voyage autour du monde exécuté par ordre du roi sur la corvette La Coquille* (Journey around the world on the corvette La Coquille, Paris, six volumes, 1826–1830), including new records of lizards and amphibians from Chile. Under *Calotes chilensis* (Lesson 1830) (Fig. 1.1b) was described a lizard that will later be the genotype of the *Liolaemus* (Wiegmann 1834) genus (Donoso-Barros 1966).

The first German zoologist that played an important role in the study of Chilean herpetology was Arend Friedrich August Wiegmann, who was born in Brunswick (Braunschweig), Germany, on June 2, 1802. He studied medicine and philology at the University of Leipzig but then focused his work in zoology, more specifically in the areas of mammalogy and herpetology. His studies with the herpetofauna species from Chile are from 1835, when the Prussian physician and botanist Franz Julius Ferdinand Meyen collected several specimens on his journey around the world between 1830 and 1832. In Argentina there is a lizard species *Liolaemus wiegmannii* (Duméril and Bibron 1837) named in his honour (Fig. 1.1c).

Years after France sent their first expedition, three renowned French naturalists and explorers played an important role in this story. They are Claude Gay, Charles Gaudichaud-Beaupré and Alcide d'Orbigny, who sent several specimens (frogs and lizards) from Chile to the zoologist André Marie Constant Duméril and to his assistant Gabriel Bibron, who worked at the Muséum National d'Histoire Naturelle in Paris, France (National Museum of Natural History in Paris, France). The identification of these species led to the publication of *Erpétologie générale, ou, Histoire naturelle complète des reptiles* (General Herpetology, or, Complete Natural History of Reptiles) in 1836 (Donoso-Barros 1966; Ortiz 2008). Alcide d'Orbigny brought from South America several specimens of lizards, among other vertebrates, which he gave to the National Museum of Natural History in Paris in 1838. Bibron was in charge of describing several specimens while writing with Duméril General Herpetology. Nine years later, when Bibron died of tuberculosis, d'Orbigny had to finish the publication (Lescure et al. 2002) even though he wasn't a herpetologist, which made him fail on this task publishing very little information on these new specimens, and there was no publication of them until 2002 (see Lescure et al., for more information). Some of the lizard specimens collected in Chilean Patagonia were *Liolaemus chiliensis* (Lesson 1830), *Liolaemus fitzingeri melanops* (Burmeister 1888), *Liolaemus nitidus* (Wiegmann 1834) and *Liolaemus wiegmannii* (Duméril and Bibron 1837). On the other hand, around the borders of Río Negro Province we can name only one species collected from Argentina, *Leiosaurus fasciatus* (d'Orbigny and Bibron 1837). As a result, it was for his contributions to science that the Société de Géographie in France awarded d'Orbigny with the Grand Prize in 1835, being the only naturalist traveller of the Museum to have obtained this distinction (Lescure et al. 2002). Johann Jakob von Tschudi was a Swiss naturalist who visited the National Museum of Natural History in Paris while he was writing his book. During that time, in 1938, he had the chance to work with specimens from Chile, which led him to the description of new specimens of amphibians and reptiles.

In 1838, Johann Ludwig Gravenhorst, a German naturalist, described *Liolaemus lemniscatus* for Argentina and Chilean Patagonia. Although he had never been to Chile, he created the genera *Phymaturus* (Gravenhorst 1838), to which he assigned the single species: *Phymaturus palluma* (Molina 1782). Charles Darwin collected this specimen in Chile according to Bell's description but at that time boundaries between countries were not as precise as they currently are, and other authors (Cei and Videla 2002) suggested that Darwin collected this type of specimen in Argentina during his 1835 trip. But after some years of confusion and uncertainties, this issue was very clearly solved by Lobo and Etheridge (2013) with a redescription of *P. palluma*.

The Zoology of Voyage of the Beagle by the well-known British naturalist Charles Darwin published between 1838 and 1843 is the result of his second expedition in the survey ship HMS Beagle, as part of a British survey expedition that included the HMS Adventure. This book includes a chapter about reptiles, written by the English zoologist, surgeon and writer Thomas Bell, an excellent contribution to South American herpetology (Donoso-Barros 1966). It contains excellent and accurate descriptions of specimens and locations (Keynes 2000) as well as of numerous new species for all over Patagonia that can currently still be found, such as *Liolaemus bibronii* (Bell 1843), *L. fitzingerii* (Bell 1843), *L. gracilis* (Bell 1843), *L. kingii* (Bell 1843), *Diplolaemus bibronii* (Bell 1843), *D. darwinii* (Bell 1843), *Stenocercus pectinatus* (Duméril and Bibron 1835) and in both countries *Proctotretus pictus* (Duméril and Bibron 1837) and *Proctotretus chiliensis* (Lesson 1830), now *Liolaemus*.

The southernmost lizard in the world, *Liolaemus magellanicus* (Fig. 1.1d), was described in 1847 by two French surgeons and naturalists, Jacques Bernard Hombron and Honoré Jacquinot. We can still find today in Patagonia (in both countries) this species that was collected by them in the expedition *Voyage au Pôle Sud et dans l'Océanie sur les corvettes l'Astrolabe et la Zélée* (Trip to the South Pole and Oceania on corvettes Astrolabe and Zélée).

Charles Frédéric Girard, a French biologist (naturalized as a US citizen in 1854) specialized in ichthyology and herpetology, and Edward Drinker Cope, an American paleontologist and anatomist, studied many species from Chile. The United States of America led three important expeditions to South America in order to collect different types of data, from biological information to geography, government, social condition, mineral and agricultural resources, among other topics, which were collected by the "US Naval Astronomical Expedition to Chile" (1854), the "US Exploring Expedition" (1855) and the "US Fish Commission Streamer Albatross" (1876) years before.

Rudolph Amandus Philippi was a German paleontologist and zoologist, who was invited to Chile by his brother Bernhard Eunom Philippi. He used to work for the Chilean government. He moved to Santiago de Chile, in 1851, where he became a professor of botany and zoology and the director of the Natural History Museum. Rudolph Philippi described three new species of South American lizards (Ortiz 2008).

One more German naturalist, Karl Hermann Konrad Burmeister, was born in Stralsund, Germany, on January 5, 1807. He graduated in medicine in 1829 and received his doctorate in philosophy. He acted as a surgeon in the mandatory military service in Germany but then decided to devote himself to natural sciences. There, he started teaching zoology at Martin Luther University in Halle in Saxony-Anhalt. His first research works dealt with entomology (Schneider et al. 2014). He was a very prolific author, and his works covered not only zoology but also botany, paleontology and geology (Schneider et al. 2014). Thanks to the academic and economic support of the famous German naturalist and explorer Alexander von Humboldt, in 1850, Burmeister was able to travel to Brazil, visiting the states of Rio de Janeiro and Minas Gerais and returning to Germany in April 1852, with all the material he collected during his expeditions. In 1857 he returned to South America, visiting the city of Buenos Aires, Argentina, from where he made several trips to different locations of Argentina. Burmeister identified quickly with this country, where he made many important contributions to biological, geological and paleontological studies and also to his private life because he got married and started a family. In February 1862, he was appointed Director of the Museum of Buenos Aires in the city of Buenos Aires, a position that he would hold until his death on May 8, 1892. Amidst his various studies Burmeister also dealt with reptiles, describing at least six currently recognized species, among them, a Patagonian lizard *Liolaemus melanops* (Burmeister 1888). In 2012, Avila et al. described a new species of lizard for Neuquén Province in Argentina honouring the German naturalist: *Liolaemus burmeisteri* (Avila et al. 2012; Fig. 1.1e).

Another French zoologist and herpetologist, Fernand Lataste, arrived to Chile by the end of the nineteenth century. His most important contribution to Chilean herpetology was the book published in 1891: *Etudes sur la faune chilienne* (Studies on Chilean Fauna). Between 1862 and 1866, the Pacific Scientific Commission took place (Macía and B. F. de Caleya 2008). This was the largest expedition that the Spanish monarchy financed at that time, where a group of naturalists and a photographer travelled extensively through South America to study the biota of the southern countries (Macia and Blanco 2008). The specimens that were collected in this voyage led Marcos Jiménez de la Espada, a Spanish zoologist, to describe seven new species in Chile.

There is an important Belgian naturalist who never travelled to Patagonia to collect material but described many specimens collected in the area: George Albert Boulenger. In 1880, he began working in the Natural History Museum in London and is nowadays the scientist who had described the most reptile taxa worldwide (Uetz and Stylianou 2018).

Julio Germán Koslowsky, who is considered the first Argentinean herpetologist, was born in Steinholm, Latvia, on September 15, 1866 (Fig. 1.1f). He belonged to a noble and wealthy family that gave him the possibility to be a very cultured person, speaking nine languages and possessing a great knowledge of botany, zoology, geology and medicine. In 1886, when he was 20 years old, he travelled to Buenos Aires. During his first years in Argentina, he worked as a teacher. In addition, in 1892 he began working at the Museo Argentino de Ciencias Naturales de Buenos Aires (Argentinean Museum of Natural Sciences of Buenos Aires), now known as the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (Argentinean Museum of Natural Sciences "Bernardino Rivadavia") as an assistant. In 1894 he became an explorer for the Museo de La Plata (Museum of La Plata), located in La Plata City (Fig. 1.1g). As a member of the Museum of La Plata, and collaborator of the founder and Director of this museum, Francisco P. Moreno, he travelled through many regions of Argentina from north to south. He also explored other countries such as Bolivia, Paraguay and Brazil, visiting unexplored places, where he made important ethnographic research and collected material of all kinds for the museum (Williams and Aguado 2006). During the summer of 1895–1896, Koslowsky, together with the engineer and topographer Teodoro Arneberg, explored the southwestern region of the Argentinean Province of Chubut, northwest of Santa Cruz and part of Puerto Aisén, territory currently belonging to Chile. He also explored the Lake La Plata and he was the first white man to reach its western end (Aguado and Williams 2003). He was also a pioneer explorer in the surroundings of the region where the Chilean city of Coyhaique is nowadays located. In his trips, he captured an important number of amphibians and reptiles, and this material was the foundational basis of the Herpetology Collection of La Plata Museum (Ferraro and Williams 2006). As a result of the analysis and study of the collected specimens, he published the description of 11 species of lizards, four for Patagonia, *Liolaemus boulengeri* (Koslowsky 1898), *Liolaemus elongatus* (Koslowsky 1896), *Phymaturus patagonicus* (Koslowsky 1898; Fig. 1.2a, b) and *Liolaemus multicolor* (Koslowsky 1898), and three species of snakes, which are still recognized today. Only a few remains of his notes are found today; as a small treasure we include here the first page of his manuscript for MLP printers of his 1896 paper (Fig. 1.3a). Some of the reptiles collected by Koslowsky on that trip were studied many years later and proved to be new species, *Liolaemus exploratorum* (Cei and Williams 1984), a still enigmatic and never found again species of the northwestern corner of Santa Cruz Province, in Argentina (Fig. 1.3b). After living several years in Patagonia, in 1916 he returned to Buenos Aires. In 1921 he went back to Patagonia, where he settled in his little ranch near the town "Lago Blanco" in the southwest of the Province of Chubut. There, he died on September 23, 1923. His remains lie in that place (Fig. 1.3c).

Even though European naturalists have been the most interested in Patagonia, there is an American paleontologist, named John Bell Hatcher, that made several expeditions to this southern land between 1896 and 1899 (Haller 2004). During his fieldtrips, he took notes of the geography, fauna and flora of the region and collected specimens later deposited in the United States National Museum. Brown (1903) quotes Hatcher's notebooks from Patagonia north of the Santa Cruz river, where he writes that he has seen a great variety of lizards in size, colour and shape. This is

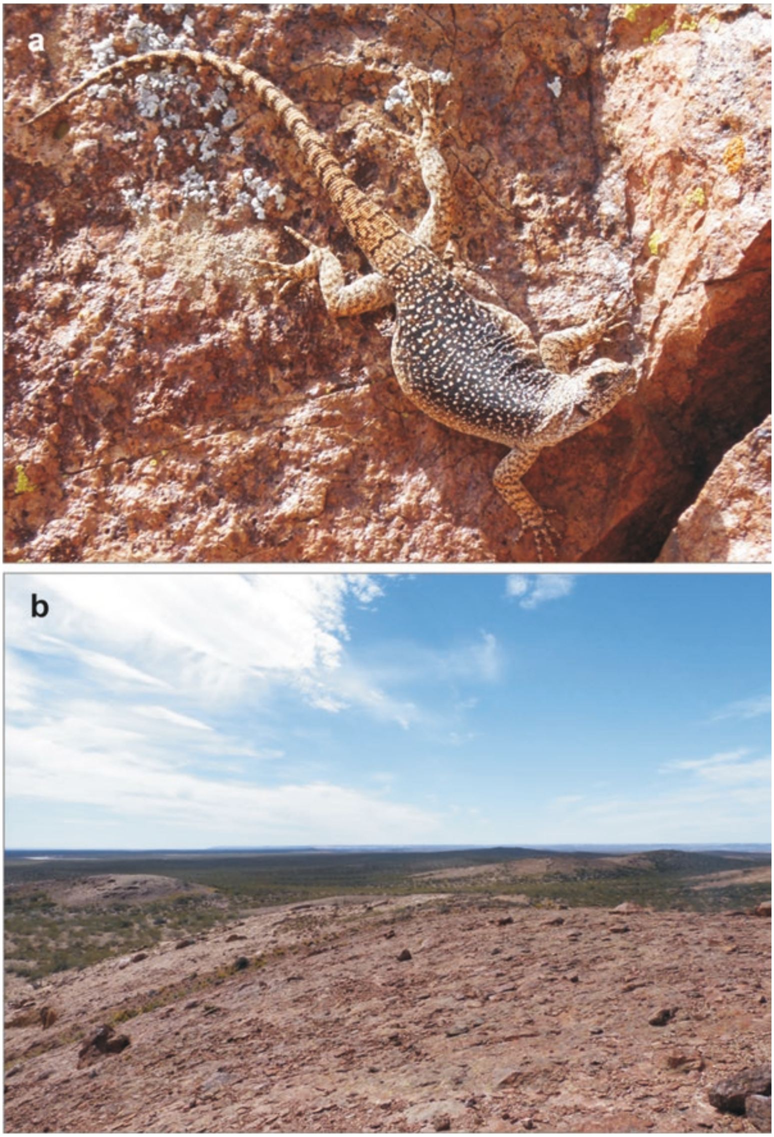


Fig. 1.2 (**a**) *Phymaturus patagonicus* from the type locality, 40 km W Dolavon, Chubut Province, Argentina; (**b**) a general view of the type locality. This is the unique locality of the lizards described by Koslowsky (1896) with an accurate geographic precision after a careful research made by Lobo and Quinteros (2005)

why in 1909 Stejneger describes a new species of lizard from Patagonia, collected by Hatcher in 1898, with the name *Liolaemus hatcheri* in his honour (Fig. 1.3d, e). Many years later, Richard Etheridge (Figs. 1.3f and 1.4a) would redescribe this species (Etheridge 1998).

Enumeracion sistemática y distribucion geográfica de los reptiles argentinos. 1
por Julio Koslowsky.

Este trabajo está basado sobre la clasificacion exacta de los reptiles reunidos hasta ahora en los diferentes establecimientos científicos de la República, al cual contribuye el abundante material del Museo de La Plata.

Fig. 1.3 (**a**) Handwriting made by J.G. Koslowsky for its paper about Argentinean reptiles (1898), courtesy of Museo de La Plata Library; (**b**) *Liolaemus exploratorum*-type specimen at MLP herpetological collection; (**c**) Graveyard of J.G. Koslowsky near Lago Blanco, southwestern corner of Chubut Province, Argentina, who is the only one herpetologist resting in Patagonian soil; (**d**) *Liolaemus hatcheri*-type specimen at Smithsonian Institution at Washington, DC, USA; (**e**) *Liolaemus hatcheri* from Santa Cruz Province, Argentina; (**f**) Richard E. Etheridge (left) with J.D. Williams at the IV Congreso Latinoamericano de Herpetología, Santiago de Chile, 1996

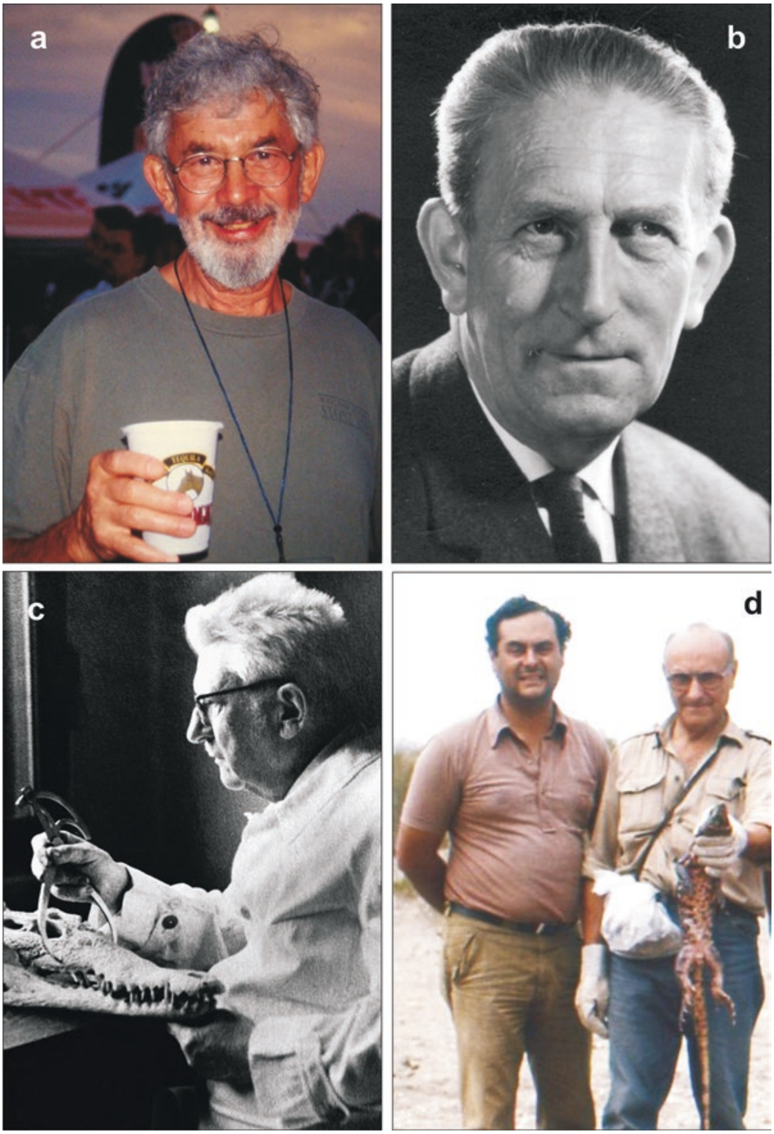


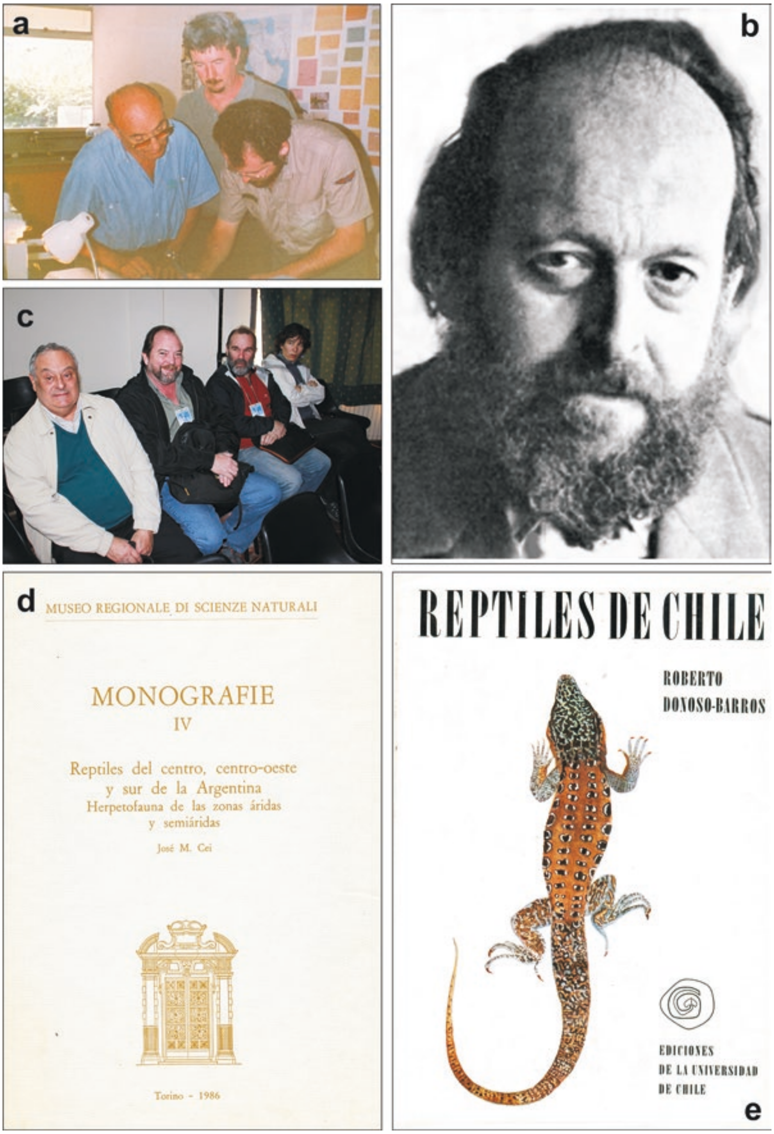
Fig. 1.4 (**a**) Richard E. Etheridge at Joint Meeting of Ichthyologists and Herpetologists 2000, La Paz, Baja California Sur (Courtesy of R. Montero); (**b**) Walter Hellmich (Zoologische Staatssammlung München [ZSM], courtesy of Frank Glaw); (**c**) Lorenz Müller (Zoologische Staatssammlung München [ZSM], courtesy of Frank Glaw); (**d**) J.A. Scolaro and J.M. Cei (handling a *Salvator rufescens*) at Valcheta, Río Negro Province, Argentina, 1980 (Courtesy of J.A. Scolaro)

Walter Hellmich (Fig. 1.4b) was a herpetologist born in Oschatz, Germany. He was able to secure a job in München, Germany, before the Second World War and work in cooperation with Lorenz Müller (Fig. 1.4c). He travelled to Chile and brought back to Germany a large collection of reptiles, some of which he obtained from W. Schröder, through Johann Goetsch, and for several years studied the Andean lizard fauna. Müller and Hellmich made important contributions describing specimens collected mainly in Chile, as well as some from Argentina (*L. kriegi*, *L. goetschi*), and still deposited in the Zoologische Staatssammlung in München (for more information see Franzen and Glaw 2007). They made some interesting contributions to high Andes Chilean herpetofauna related mostly to systematics and evolution of *Liolaemus* genus, describing some still very complex species, like the *Liolaemus monticola*, *L. villaricencis*, *L. chillanensis* or *L. tenuis* complexes. Hellmich (1934, 1951, 1952) wrote the first synthesis works on the genus *Liolaemus* and stated that the *Liolaemus* genus may have been originated from Tierra del Fuego and had been differentiating in the Andes as they elevated, altering territorial extensions and constrains with fragmentation and differentiation depending on the glacial and interglacial fluctuations. In these papers he writes that after he stayed in Chile he was able to "intensively collect" specimens and with other contributions a large amount of material had been accumulated in the Zoologische Staatssammlung (Zoological State Collection) in München, Germany, from Patagonian lizards.

1.4 A New Era: The Rise of the First "Local" Researchers

The Chilean herpetologist R. Donoso Barros (Fig. 1.5b) undoubtedly influenced the researcher that made the greatest contribution to the knowledge of Patagonian lizards: José Miguel Alfredo María Cei (Figs. 1.4d and 1.5a). Cei was born in the Italian commune of San Miniato, in the Province of Pisa, in 1918. In 1940 he acquired his Doctorate in Biological Sciences (Zoology). Later, he became a Professor at the University of Florence between 1942 and 1947. When he left his position at the University of Florence (1947), he was hired as Professor of General Biology at the National University of Tucumán, in Argentina, the country whose citizenship he adopted in 1952. He held several positions at the University of Tucumán, and his scientific contributions to herpetology during this period focused on the Sexual Cycles and Biology of Amphibians.

Five years later, in 1957 he was in charge of the organization of the Department of Ecology of the Universidad de Chile (University of Chile). There he carried out numerous investigations on Chilean herpetofauna, highlighting his monographic work *Batracios de Chile* (Chilean Batrachian). Between the years 1955 and 1958, he moved to the city of Mendoza, where he obtained the position of Professor in the Scientific Research Department at the Universidad Nacional de Cuyo (National University of Cuyo) and remained there until his retirement in 1980. During these 25 years, he occupied various positions, among which we can remark Director of the Institute of Animal Biology, Director of the Department of Morphology in



MUSEO REGIONALE DI SCIENZE NATURALI

MONOGRAFIE
IV

Reptiles del centro, centro-oeste
y sur de la Argentina
Herpetofauna de las zonas áridas
y semiáridas

José M. Cei

Torino - 1986

REPTILES DE CHILE

ROBERTO
DONOSO-BARROS

EDICIONES
DE LA UNIVERSIDAD
DE CHILE

Fig. 1.5 (**a**) From left to right, José Miguel Cei, Ricardo A. Martori and Luciano J. Avila, working on the description of *L. saxatilis* at Universidad Nacional de Río Cuarto, 2001; (**b**) Roberto Donoso Barros (Courtesy of A. Labra); (**c**) from left to right, José A. Scolaro, J.D. Williams, Felix B. Cruz and Gabriela Perotti at the XII Congreso Argentino de Herpetología, 2012, Bariloche, Río Negro Province, Argentina; (**d**) monograph on Argentinean Patagonian reptiles by J.M. Cei (1986); (**e**) book by R. Donoso-Barros, *Reptiles de Chile* (1966)

Medical Sciences and Director of the Department of Postgraduate in Agricultural Sciences. During that time, he developed an intense activity, teaching and researching mainly Patagonian herpetofauna. A tenacious traveller and an enviable explorer of nature, Cei was the author of the description of many species of amphibians and reptiles. He published an enormous amount of papers and several books that even today are a very valuable corpus of bibliography of obligatory consult. These books are as follows: *Anfibios de Argentina* (Amphibians of Argentina) 1980, *Reptiles del Centro, Centro Oeste y Sur de la Argentina* (Reptiles of the Centre, Centre-West and South of Argentina) 1986 (Fig. 1.5d), *Reptiles del Noroeste, nordeste y Este de la Argentina* (Reptiles of the Northeast and Northwest of Argentina) 1993 and *Anfibios de la Argentina* (Amphibians of Argentina), a Second Update (1987–2000 in collaboration with E. Lavilla). He was a great "connoisseur" of other areas of science such as geology, paleontology, paleoclimatology and botany, a permanent generator of ideas guiding the direction of research in different areas. In recognition of his important work, he received a large number of special mentions, awards and honorary doctorates all over the world, especially in Argentina. Cei participated, alone or in co-authorship, in the description of 52 species of amphibians and 50 species of reptiles, 46 of which are lizards, mostly Patagonian. The main collaborators in the study and description of new species of Patagonian lizards were his disciples Fernando Videla and Alejandro Scolaro (Figs. 1.4d and 1.5c). Despite being a recognized specialist in the ecology of Antarctic and Patagonian birds, Scolaro's relationship with J.M. Cei led him to devote himself more and more to the study of Patagonian lizards. Therefore, he published a large number of articles especially referred to the taxonomy of the lizards of Patagonia, summarizing years of work in two field guides of the reptiles from this region in 2005 (south Patagonia) and 2006 (north Patagonia). Scolaro worked several decades in the Patagonian National Center (CENPAT-CONICET) until his recent retirement.

In this account, we cannot forget the leading Chilean scientist Roberto Donoso-Barros (Fig. 1.5b), whose pioneering research on herpetofauna led into numerous and important publications in matters as taxonomy, physiology and reptile ecology. In 1966, he published his main work, *Reptiles de Chile* (Reptiles from Chile) (Fig. 1.5e), covering all known current terrestrial and marine species, with a review regarding most of the existing literature where he also described new reptile and amphibian taxa for the entire country.

Jose M. Gallardo was an Argentinean zoologist who dedicated his life to the study of amphibians and reptiles (Lajmanovich 2005). He published many articles, specimen identification guidebooks and systematics papers, among other manuscripts (Gallardo 1994; Lajmanovich 2005). Gallardo, in 1970, made a checklist of the lizards for Argentinean Patagonia with a brief description and distribution information. In 1971, he published a more extensive manuscript, entitled "The zoogeography of Patagonian Saurian", concluding that at that moment there were a total of 16 lizard species for this area (Gallardo 1971).

The first female herpetologist in Chile was Maria Codoceo, who travelled through the entire Chilean territory, searching for new reptile species to describe. At the same time, she was a devoted teacher; she worked at the Museo Nacional de

Historia Natural de Chile (National Museum of Natural History of Chile). She was also a member of the Sociedad Chilena de Historia Natural (Chilean Society of Natural History) taking special care of the herpetological collection at the Museum. Later she would make contributions to this collection with the species gathered in her different fieldtrips. Between 1951 and 1956, she held an unpaid position as the Chief of the Reptile Section. She received the recognition of prominent herpetologists, as well as José Miguel Cei and Roberto Donoso-Barros. She was also an outstanding malacologist. Between 1950 and 1978, Codoceo published her contributions in the Informe Mensual del Museo Nacional de Historia Natural (Monthly Report of the National Museum of Natural History), and in Issue Number 4, corresponding to November 1956, Codoceo made a description of the species held in Herpetology Section (San Martín and Vidal Maldonado 2013).

Raymond Laurent (Fig 1.6a), in 1983, made one of the most important contributions in the study of the genus *Liolaemus*. Although he worked mainly with lizard species from northern Argentina, he was the first to make a more methodological approach to understand the evolution and phylogenetic relationships of the genus *Liolaemus*. In several key papers published in the early 1980s, he recognized the two big evolutionary lineages in the genus, the *Eulaemus* (The Argentino Group, Fig. 1.6b) and the *Liolaemus* (The Chileno Group, Fig. 1.6c), now more accepted as subgenera. He was the first to use a morphometric statistical method to study and recognize those evolutionary lineages in an academic world that was just ignored or starting to use them with some doubts and/or lack of trust (Laurent 1983, 1984, 1985). He managed to create a large academic lineage of herpetologists in the Fundación Miguel Lillo (Fig. 1.6d); several of them made significant contributions to the Patagonian herpetology. An American researcher, Richard E. Etheridge, working initially with J.M. Cei, and later with some members of the Laurent group, M. Christie, or alone, made important contributions to the systematics of several groups of *Liolaemus* and *Phymaturus*, as well as to clarify some nomenclatural, taxonomic or phylogenetic problems in those genera.

1.5 The Current Situation

Undoubtedly, the creation of the Asociación Herpetológica Argentina (Argentine Herpetological Association) in 1982 gave a great boost to herpetological studies throughout the country, establishing new links among Argentine scientists and promoting the discipline among new generations of biologists (Williams 2007, 2013).

After 2004, a study group is set up in the city of Puerto Madryn, Province of Chubut, Argentina. This group, now in the Patagonian Institute for the Study of Continental Ecosystems (IPEEC-CONICET), focuses on the study of systematics and evolution of Patagonian lizards, led by Luciano J. Avila and Mariana Morando that created the Patagonian Herpetological Group-Systematic, Biogeography and Evolutionary Biology Lab (GHP-LASIBIBE), where several students made significant studies on Patagonian lizards, including Andrea González Marín, Cintia

Fig. 1.6 (**a**) Raymond Laurent (Courtesy of R. Montero); (**b**) *Liolaemus goetschi*, from Cerro Policía, Río Negro Province, Argentina, a member of the *Eulaemus* subgenus (Courtesy of I. Hernandez); (**c**) *Liolaemus gununakuna*, from Cerro Lotena, Neuquén Province, Argentina, a member of the *Liolaemus* sensu stricto subgenus (Courtesy of I. Hernandez); (**d**) Raymond Laurent with some of its disciples: marked with red arrows only those with relationships with Patagonian lizards; from left to right, upper, F.B. Cruz, R. Montero, G.J. Scrocchi, F. Lobo; in the middle, V. Abdala; at her left, G. Perotti

Medina, Cristian H.F. Pérez, Florencia Breitman, Ignacio Minoli, Melisa Olave and Paula Escudero, among others (Fig. 1.7a, b). Without any doubt, Jack W. Sites Jr. (Fig. 1.7b, c) from Brigham Young University was a strong supporter in the study of Patagonian lizards working together with the GHP-LASIBIBE during the last 20 years.

In the city of San Carlos de Bariloche, Río Negro Province, there are two other research groups in the Research Institute in Biodiversity and Environment (INIBIOMA-CONICET), one led by Nora Ibargüengoytia (Fig. 1.8a) and the other by Félix Benjamín Cruz and Gabriela Perotti (Figs. 1.5c and 1.6d), whose research is associated with topics related to the physiology, behaviour and ecology of the Patagonian herpetofauna, mainly lizards. Both groups managed to create their own descendant of herpetologists, including Debora Moreno Azocar, Erika Kubisch, Jorgelina Boretto, Marcelo Bonino and Marlin Medina. Nora Ibargüengoytia's group is a leading one in studies on reproduction and thermal ecology for Patagonian lizards and with American colleagues as Barry Sinervo (UCSC) and Donald Miles (OU) made significant contributions through collaborative projects.

From his relationship with the Argentinean National Parks Administration, Miguel Christie (Fig. 1.8b) collected very important data on the distribution and biology of lizards of Patagonia, particularly in the area included within the National Parks Lanín and Nahuel Huapi, published in internal reports and in scientific articles. He worked closely with Richard Sage, who managed to create one of the largest collections of *Liolaemus* outside South America at the Museum of Vertebrate Zoology in Berkeley, USA. Unfortunately, this large amount of collected material was only followed by a modest number of publications.

Among the researchers located outside the Patagonian region, two that are part of the academic lineage of Raymond Laurent, are Fernando Lobo (IBIGEO-CONICET) (Figs. 1.6d and 1.7d, e) and Cristian Abdala (FML-CONICET) (Fig. 1.7d). They made significant contributions to the systematic of the Patagonian lizards describing a large number of *Phymaturus* and *Liolaemus* species and studying systematic relationships mainly focused on morphological traits. Other researchers that made contributions on some aspects of biogeography, systematic and ecology of some Patagonian lizards are as follows: Valeria Corbalán (biogeography, conservation, IADIZA-CONICET) (Fig. 1.8b), Sebastian Quinteros (morphological taxonomy, IBIGEO-CONICET), Juan Carlos Acosta (ecology, UNSJ), Gustavo Scrocchi (FML-CONICET) (Fig. 1.6d), Ricardo Montero (Amphisbaenians, UNT) (Fig. 1.6d) and Virginia Abdala (morphology FML-CONICET) (Fig. 1.6d).

In Chile we must highlight the invaluable contributions to the knowledge of Patagonian lizards made by Juan Carlos Ortiz (Fig. 1.9a), Alberto Veloso and Herman Antonio Nuñez, along with his numerous collaborators. Now a new generation of Chilean herpetologists, including Pedro Victoriano (Fig. 1.9b), Antonieta Labra, Marcela Vidal, Fernando Torres Perez as well as some of their successors as Jaime Troncoso Palacios and Damien Esquerré with a large group of collaborators, is making a very significant progress on the systematics, phylogeny, ecology, behaviour and other aspects of lizards of the western side of the Andes. The contributions of Antonieta Labra Lillo and Marcela A. Vidal Maldonado should be highlighted,

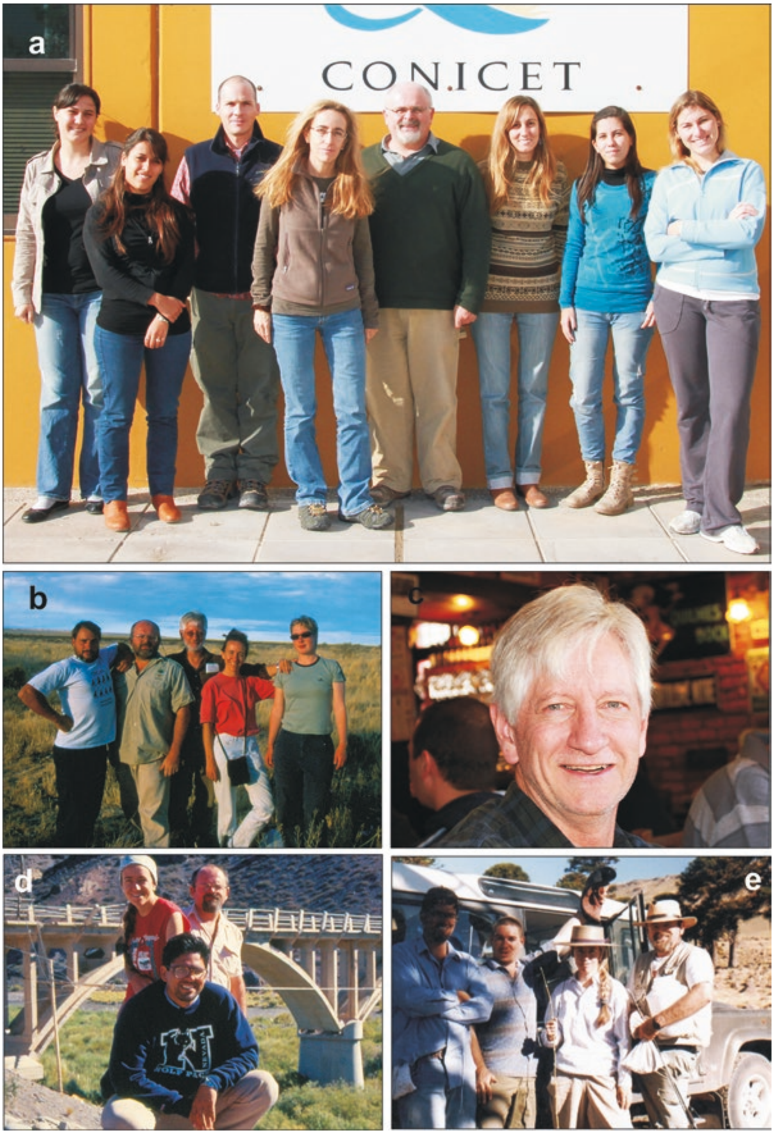


Fig. 1.7 (**a**) Grupo de Herpetología Patagónica (GHP-LASIBIBE), 2012, from left to right: M. Olave, P.C. Escudero, I. Minoli, M. Morando, L.J. Avila, C.D. Medina, M.A. González Marin and F. Breitman; (**b**) GHP-LASIBIBE in 2003, from left to right: C.H.F. Perez, L.J. Avila, J.W. Sites, Jr., M. Morando and K. Dittmar, in southern Mendoza Province; (**c**) J.W. Sites Jr. at the XII Congreso Argentino de Herpetología, 2012, Bariloche, Río Negro Province, Argentina; (**d**) M. Morando, L.J. Avila (back) and F.J. Lobo Gaviola, after crossing the Barrancas River, fourth January 1999, Neuquén Province, Argentina; (**e**) from left to right: F.J. Lobo Gaviola, C.S. Abdala, M. Morando and L.J. Avila, in the Araucaria Forest, January 1999, Neuquén Province, Argentina (Courtesy of C.S. Abdala)

Fig. 1.8 (**a**) Members of the Nora Ibargüengoytia Lab at the INIBIOMA-CONICET-UNCOMA, San Carlos de Bariloche, Río Negro, Argentina; from left to right: Mariela Fernández, Marlin Medina, Facundo Cabezas-Cartes, Nora Ibargüengoytia, Jimena Fernández (up), Jorgelina Boretto, Fernando Durán, Erika Kubisch, Nicolas Ceccheto; (**b**) Guillermo Debandi, Valeria Corbalán and Miguel Christie at the XII Congreso Argentino de Herpetología, 2012, Bariloche, Río Negro Province, Argentina; (**c**) Antonieta Labra (left) and Marcela Vidal (right) at the IX Congreso Argentino de Herpetología, San Luis, 2008; (**d**) book *Herpetología de Chile* by A. Labra and M. Vidal (eds)

Fig. 1.9 (**a**) Juan Carlos Ortiz at the IX Congreso Argentino de Herpetología, San Luis, Argentina, 2008; (**b**) Pedro Victoriano at the IX Congreso Argentino de Herpetología, San Luis, Argentina, 2008; (**c**) Herman A. Nuñez (Courtesy of H.A. Nuñez); (**d**) Fernando Torres Pérez (Courtesy of F. Torres Pérez); (**e**) Graciela Blanco, Juan C. Acosta y A. Labra at the X Congreso Argentino de Herpetología, Jujuy, Argentina, 2009; (**f**) Alberto Veloso with his wife Cecilia, in 2007; (**g**) from left to right: Rodrigo Silva, Damien Esquerré, Carlos Garín y Jaime Troncoso Palacios

especially the book *Herpetology of Chile* (2008), with abundant information on Chilean Patagonian lizards, a work still waiting to be done on the Argentinean side.

Working from outside South America, Daniel Pincheira-Donoso, now in United Kingdom, is an evolutionary biologist, who worked mainly with lizards, making interesting contributions in selection theory, the ecology and genetics of adaptations, macroecology, life history evolution, climate change biology and conservation.

Of course we may have forgotten some people in our review and we apologize in advance for any omissions. The history of Patagonian herpetology seems to be small but after one starts retrieving information, soon it is evident that is fascinating and very complex. Some sources are still missing in the libraries and difficult to recover; others, as Koslowsky's records, disappeared forever.

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Chapter 2
The Relationship Between People and Lizards in Patagonia

Juana Aigo, Ana Ladio, Jorgelina M. Boretto, Facundo Cabezas-Cartes, and Nora R. Ibargüengoytía

Abstract Understanding how human beings perceive and interact with the local herpetofauna is fundamental for its conservation. In this chapter, we propose looking forward to the local ecological knowledge (LEK) of the Patagonian lizards, especially the "matuasto". The preliminary analysis of ethnohistorical sources points out the relevant role of "matuastos" in the cosmologies of the original people from Patagonia, often considered as immortal, selfish and harmful beings. Field reports agree on the warning not to disturb these territorial lizards; otherwise, they would react aggressively with bites. The recorded stories account for frequent biting events on sheep. The local perception on "matuastos" as harmful beings would provoke an attitude of caution and rejection towards them. This work provides a first overview on the relationship of lizards and the people from Patagonia while constituting an initial step for future research.

Keywords Reptiles · Local ecological knowledge · Patagonia

J. Aigo (✉)
Instituto de Diversidad y Evolución Austral – Consejo Nacional de Investigaciones Científicas y Técnicas (IDEAus – CONICET), Puerto Madryn, Chubut, Argentina
e-mail: aigo@cenpat-conicet.gob.ar

A. Ladio · F. Cabezas-Cartes · N. R. Ibargüengoytía
Instituto de Investigaciones en Biodiversidad y Medioambiente, Consejo Nacional de Investigaciones Científicas y Técnicas (INIBIOMA-CONICET), San Carlos de Bariloche, Río Negro, Argentina
e-mail: ladioah@comahue-conicet.gob.ar; norai@comahue-conicet.gob.ar

J. M. Boretto
Instituto de Investigaciones en Biodiversidad y Medioambiente, Consejo Nacional de Investigaciones Científicas y Técnicas (INIBIOMA, CONICET-Universidad Nacional del Comahue), San Carlos de Bariloche, Río Negro, Argentina
e-mail: borettojm@comahue-conicet.gob.ar

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2.1 Human-Reptile Relationship

Throughout history, humans have forged a variety of bonds with animals: utilitarian, emotional and evolutionary, among others. In general, such relationships surpass the pure materialistic view to become, in most cases, rooted in a strong symbolic origin (Vargas-Clavijo and Costa Neto 2010). In particular, lizards and snakes, and also dinosaurs, have raised curiosity and great interest among people, being the topic of myths and legends passed on from parents to children since the beginning of time.

Whereas reptiles hold a central place in the media, the visual arts and the collective imagination due to the fascination these animals evoke in different societies, extremely different views towards them are clearly exposed by different cultures and societies throughout time. Reptiles were considered "abominable and repulsive" by Carl Linnaeus, father of modern systematics (Lavilla 2012). The Judeo-Christian culture associated them with the original sin since the book of Genesis; but in American cultures they played a relevant role in the worldview of their peoples (Mera and Lobos 2008), including admiration and respect. Academic research, on the other hand, produced a large body of evidence demonstrating that reptiles play a crucial ecological role as predators of insects and rodents, as prey of birds and mammals and as seed dispersers and pollinators (Valencia-Aguilar et al. 2013). Numerous research studies showed that reptiles are globally threatened by loss of habitat, diseases, pollution and extraction (Gibbons et al. 2000; Alves et al. 2008; Cox and Temple 2009; Todd et al. 2010; Böhm et al. 2013), referring to what it has been termed the "déjà vu of amphibians in reptiles", in reference to the recognized global decline of the former (Gibbons et al. 2000). Meanwhile, the general public in western cultures knows little about the ecology of reptiles or their conservation status. A closer examination at the knowledge and attitudes towards the reptile fauna would shed light on the kind of bonds particular societies developed towards them, providing elements to identify opportunities and challenges for their conservation.

Ethnozoology analyses the understanding and the different forms of handling, conserving and taking advantage of the animal resources in different societies through the study of the local ecological knowledge (LEK) (Santos Fita and Costa Neto 2007). LEK is the result of a biocultural inheritance in the communities that is constructed and reconstructed over successive generations (Alves and Rosa 2013). According to different authors (Santos Fita et al. 2009; Hermann et al. 2013; Aigo and Ladio 2016), these bonds and values based on cultural beliefs stimulate both positive and negative attitudes, which may vary from attraction to disgust or fear, from admiration to indifference, with all sorts of shades and combinations in between. These complex bonds vary in relation with a wide range of factors such as cultural affiliations, environmental context (Arango et al. 2007), age, socioeconomic status, gender, religious influence and cultural uprooting, among others (Alves and Rosa 2013).

The bonds that people and societies establish with animals, and with reptiles in particular, are complex, dynamic and flexible and finding universal patterns becomes an elusive task. Nevertheless, many ethnozoological studies have shown that in the majority of the traditional societies, animals occupy a prominent role in their spirituality and their cultural heritage, evidenced directly or indirectly by their actions in everyday life, and being part of stories and meaningful myths (Villagrán et al. 1999; Rozzi et al. 2003; Castro 2004).

In South America it is possible to find a range of examples that show the importance of animals to traditional societies. Alves et al. (2010) point out that at the same time reptiles have a wide utilitarian value, traded around the world as pets, good luck charms and medicine; they are also considered as harmful animals and associated with evil and as real pests and for those reasons hunted and killed (Alves et al. 2009b; Araujo and Luna 2017). For example, in Brazil, the "teiús" (*Salvator merianae* and *S. teguixin*) are frequently killed to prevent them from eating chicken eggs and chicks, as well as using them as food, ornamentation and medicine (Alves and Rosa 2006; Alves et al. 2009a, 2010; Confessor et al. 2009; Ferreira et al. 2009). Similarly, poisonous snakes such as the rattle (*Caudisona durissa*), coral (*Micrurus* sp.) and yarará (*Bothrops leucurus*) are killed to prevent attacks to domestic animals and people, and their fat used in home remedies (Alves and Rosa 2006). It is estimated that 53% of the zoopharmacopoeia in Brazil is composed of reptiles (Alves et al. 2008). In the Andes, the use of reptiles in rituals and traditional medicine is part of the native customary rights acquired by local indigenous communities. In the Puna ecoregion in Argentina, Bolivia and the Chilean Altiplano, the tail of a lizard (*Liolaemus* sp.) is used for curdling milk and prescribed for relieving the pain in broken bones (Barbarán 2004; Mera and Lobos 2008). Barbarán (2004) also highlights the use of fat of the snake *Tachymenis peruviana* to alleviate swellings and pain in the kidneys and bones. In Peru and Bolivia, lizard oil is widely used as a powerful tonic for lung diseases, effective against snoring and anaemia. In rural areas of Bolivia, lizards are used as "patches" to cure broken bones and injuries from falls (Mera and Lobos 2008).

At the present the view of reptiles and other animals within traditional societies is beginning to seriously deteriorate and fade. For example, Sanchez (2006) was able to record how the influence of the Catholic religion and other factors on an indigenous community in Mexico had favoured a massive aversion to rattlesnakes (*Crotalus triseriatus* and *Sistrurus ravus*).

2.2 Positive and Negative Connotations of Reptiles

In modern societies, regular people are not very knowledgeable about reptiles, but they naturally attribute them different characteristics, positive and negative. Lizards seem to evoke more sympathy than snakes. For example, lizards are usually considered a symbol of good omen or good luck and as animals that warn, alert and protect from evil. In places like Brazil, Hawaii or Thailand, the presence of geckos is a sign of good luck. Also, iguanas are often a symbol of joy. Likewise, in modern urban societies with less contact with nature, due to misinformation or misconceptions, there is usually a strong aversion to reptiles, which are frequently considered disgusting, dangerous and/or repulsive (Moncada et al. 2002; Alves et al. 2010).

Kellert (1996) points out that, along with fish and invertebrates, reptiles are the animals most rejected by people, dangerous combinations of negative associations that may put their survival at risk. In this context, it is crucial to mitigate false ideas about their biology and behaviour. For example, it is common for people to consider lizards as poisonous, but there are only two species of venomous and potentially dangerous lizards known to science: the lizards known as Gila monsters, *Heloderma horridum* and *Heloderma suspectum*. Both inhabit the south of USA and north of Mexico exclusively but they are very rarely seen and they are not aggressive (Beck 2005). Paradoxically, there is a substance in the saliva of these species, exendin-4, of great importance to medicine since it has been proven helpful for the treatment of diabetes type II. Exendin-4 stimulates insulin production in response to raising blood glucose levels and inhibits glucose release in the liver after feeding (Kolterman et al. 2003; Nielsen et al. 2004). Another example is the Komodo dragon (*Varanus komodoensis*), considered poisonous. Because of its highly developed immune system, the Komodo dragon can carry many different bacteria and occasionally infect people that get in contact with it. Understanding the natural defensive mechanisms of these species could contribute to answer fundamental questions in medicine about immunity and infectious diseases in humans. Unfortunately, the Gila monster is at the edge of extinction (Hammerson et al. 2007) and the Komodo dragon is ranked as a vulnerable species worldwide (World Conservation Monitoring Centre 1996).

2.3 Reptiles and People in Patagonia

The main families of lizards of Patagonia have been heterogeneously studied in terms of their ecology and biology, mostly their thermophysiology and reproductive aspects (Ibargüengoytía et al. 2005, 2016; Boretto and Ibargüengoytía 2009; Boretto et al. 2014a, b; Medina and Ibargüengoytía 2010; Duran et al. 2018; Fernández et al. 2018; Cabezas-Cartes et al. 2015, 2018), but the relationship between reptiles and local societies has seldom been analysed. Considering the lack of deep ethnozoological research, we undertook an analysis of information coming from different documentary sources and fields of study as a first approach in reconstructing the role and importance of reptiles for past and present societies in Patagonia. In this context, the wealth of dinosaur fossil localities in Patagonia, one of the most relevant territories in palaeontology today (Porfiri 2009; Casas 2000), is truly paradoxical. Some of these fossils have been found, thanks to the information provided by rural people and local experts; for example, the largest dinosaur in the world, *Patagotitan mayorum*, a giant herbivore that lived 100 million years ago, has recently been discovered in the Province of Chubut, Patagonia Argentina (Carballido et al. 2017). In the Cueva de las Manos, Río Pinturas, UNESCO World Heritage, Santa Cruz Province, ancient rock carvings depicting a “matuasto” (a group of carnivorous and voracious lizards) have been discovered next to those of a common lizard (Gradin et al. 1976) showing that they were already incorporated as significant cultural symbols (Mera and Lobos 2008).

Fig. 2.1 Lizards represented in cave paintings of Patagonia, Northwest and Central Argentina. (**a**) Details of "matuastos" in Cueva de las Manos, Province of Santa Cruz (Photograph by Mario Sánchez Proaño and Ana B. Sánchez taken from Podestá et al. 2005a); (**b**) details of "iguana" (*Salvator* spp.) in Minas Department, Province of Córdoba (Photograph of Recalde and Berberián taken from Recalde and Berberián 2005); and (**c**) details of lizards in Sierra de Carahuasi, Province of Salta (Photograph by M. Sánchez Proaño and A. B. Sánchez taken from Podestá et al. 2005b)

Similar representations were found outside of Patagonia in both Argentina (Recalde and Berberián 2005; Podestá et al. 2005b; Berberián and Nielsen 2001) and Chile (Mera and Lobos 2008; Kligmann and Díaz País 2007) suggesting their frequent occurrence in the social practices of human groups (Recalde 2009) (Fig. 2.1).

The cosmologies of the Mapuche people, as well as of other indigenous peoples of South America, consider nature as animated; both human and non-human beings inhabit their territories and share their ways of life and habits (Descola 1998; Mora 2001; Aigo and Ladio 2016). Some elements of socio-religious restrictions and taboos within these cosmologies operate as key ethical guides for the conservation of their territory (Rozzi 2016; Aigo and Ladio 2016) and as elements within traditional storytelling (Mera and Lobos 2008). For instance, it is possible to recognise snakes associated with the presence of the "nwen-ko", or protective beings of the waters in the Patagonian Andean region. According to accounts of Mapuche people in communities of the Province of Neuquén, Argentina, snakes or "culebras" and the "culebrón" inhabit and guard rivers and lakes (Aigo and Ladio 2016). These non-human beings are part of the group of animals considered as "protectors of the water" to whom permission must be asked for extracting any element from the aquatic ecosystems (Aigo and Ladio 2016). Authors such as Erize (1989) and Grebe (1971) already pointed out the "religious respect" that the Mapuche people had for snakes, considering any harm to them as an offense to the spirits. For the Mapuche people, snakes play a major role in the different versions of their creation myths. The universal flood myth tells the story of the two snakes *Treng Treng* and *Kai Kai*, who were in charge of bringing order to the Mapuche universe (Alvarez 1992; Calvo 1994; Fernández 1995; Soldano 2006; Coña 2006). Regarding this, for example, Reyes et al. (2014) pointed out the importance of lamprey (*Geotria australis*) or "Filoko" (water snake or spirit of water) as a symbolic reference for the Mapuche community of Gorbea, southern Chile. The behaviour of this fish has been regarded as close to the myth of origin and as a physical representation of the mythical snake *Kai Kai*. The lamprey is an important natural resource for food with rules and functions for the inhabitants of this community. Reyes et al. (2014) observed the fishing of lampreys as a cultural activity that is articulated to the myth of origin. Also, in a recent publication Villagrán and Videla (2018) point out the central role played by the snake image of the origin myth within Mapuche cosmology, as well as other symbolic representations of related natural elements that share some common characteristics, for example, an elongated shape, serpentine mobility, harmful potential behaviour and type of habitat. These elements can be found in Mapuche family names and lineages related to reptiles, fish or invertebrates (e.g. the worm), as well as in the names of angiosperm plants, geographical and geological features and mythical animals (Villagrán et al. 1999; Castro 2004; Villagrán and Videla 2018). In this regard, specific names in Mapudungun (Mapuche language) for lizards and snakes have been identified in Chile: "fillkuñ" and "filu", respectively. For example, both lizards and snakes can be found in some well-known family names, such as in the lineages Paynefilu (Aigo Pers. Observ), Curifilu and Millafilu (Villagrán et al. 1999). In addition, the terms "filu" and "kai kai" are identified in plants that share swampy or semi-flooded habitats, crawling or subterranean organs (tubers, stolons and rhizomes), forms of growth (leaves, flowers, fruits, seeds) and/or living conditions related to the snake (Villagrán and Videla 2018) (Table 2.1). On the other hand, the meaning of the snake "filu" and its analogous representation in figures of animals have been particularly associated with the

Table 2.1 Specific names of: (**a**) lizards and snakes, (**b**) plants and (**c**) mythical animals and (**d**) family names and lineages associated with these reptiles in Mapudungun and their meaning in Spanish

Names in Mapudungun	Meaning in Spanish	BS
(**a**)		
Fillkuñ; Vilcun	Lagartija; Lagarto/lizard (***Lspp1***)	1; 2; 3
Kirke; Querque; Lawañe	Lagarto grande; "matuasto"/big lizard (***Lspp2***)	1; 2; 3; 7
Palüm; Pallüm	Lagarto; iguana/lizard; iguana (***Cp***)	1; 2; 3
Iway; Vilo; Filu	Culebra o serpiente/snake (***Tc***)	1; 2; 3; 5
(**b**)		
Mellaufilu; milahufilu o millahuilo	"Caracol-Culebra"/"snail-snake" (**Pe**)	5
Pihuichén-lahuén	"Hierba del culebrón"/"grass of the Culebrón" (**Ca**)	5
Ühuafilu	"Maíz de la Culebra"/"snake corn" (**Jc**)	5
Ühuafilu	"Choclo de la Culebra"/"snake corn" (**Cs**)	5
Filucachu	"Mata de la Culebra"/"snake bush" (**St**)	5
Kuramfilu	"Huevos de serpiente"/"snake eggs" (**Cspp**)	5; 14
Cai	"Serpiente"/"snake" (**Gs**)	5
Filu-lahuén	"Remedio de la Culebra"/"snake medicine" (**Pf**)	5; 14
Fillcuñ-mamëll; Kalahuala	"Madera del Lagarto"/"lizard wood" (**Pf**)	5; 14
(**c**)		
Kai Kai Filu; Kai Kai Vilu	Serpiente acuática/aquatic snake	1; 2; 3; 5; 10; 12
TrengTreng Filu; TrengTreng Vilu	Serpiente terrestre/terrestrial snake	1; 2; 3; 5; 10; 12
Filokomo o Filoko	Serpiente de agua; lamprea/aquatic snake; lamprey (***Ga***)[a]	5; 6
Kurufilu	Culebra negra de agua/black water snake	5
Pichitentén	Serpiente pequeña/small snake	2; 3
Putenten	Culebra/snake	1; 2; 3
Ngürüfilu; Guirivilo	Zorro-Culebra acuática/aquatic snake-fox	3; 5
Ñarkifilu	Gato-Culebra marino/marine snake-cat	5
Cuchivilo; Cuchivilu	Cerdo-Culebra/snake-pig	3; 5
Chinifilu	Culebra-canasto/snake- basket	5
Iwaifilu; Iwai-piuchen	Serpentón ó culebrón	3; 5; 11; 14
Kaikaifilu	Dragón/dragon	5; 11
Pihuychen; Piwichen, Piuchen	Serpiente que vuela/flying snake	3; 5; 13
Piruquina	Culebra grande subterránea/large earth snake	3; 5; 9; 13
Lluhay	Reptil plateado/silver reptile	3
Vilpoñi	Lagartija de la papa grande/big potato lizard	3
(**d**)		
Nahuelquir; Nahuel Kirke	Tigre-Matuasto;Tigre-Lagartija/ snake-"matuasto"	7

(continued)

Table 2.1 (continued)

Names in Mapudungun	Meaning in Spanish	BS
Antifil	Serpiente del sol/sun snake	2; 3
Ancafil	Mitad Culebra/half snake	2; 3
Curivilu; Curivil	Serpiente negra/black snake	2; 3; 5; 8
Huenufilu	Culebra de Arriba/upper snake	2; 3
Melilfil	Cuatro culebras/four snakes	2; 3
Millafil	Culebra de oro/golden snake	2; 3
Ñancufil	Serpiente- Aguilucho/snake-harrier	2; 3
Painefil-Painefilu	Culebra Azul o celeste/blue snake	2; 3; 4
Filcún o Filún	Ser serpiente/snake being	5; 8
Filipai	Vino la Culebra/the snake came	5; 8
Filtuñanco	Serpiente-Aguilucho/snake-harrier	5; 8
Filumilla	Serpiente dorada/golden snake	5; 8
Filura	Culebra Florida/snake with flowers	5; 8
Cafil; Caifil	Una culebra más/one other snake	5; 8
Caimapo	Tierra de serpientes/land of snakes	5; 8
Caihuan	Serpiente de la tarde/afternoon snake	5; 8

Scientific names of reptiles[b] and plants[c] species as well as bibliographic sources (**BS**) are indicated below

Bibliographic sources: (1) Villagrán (1998). (2) Villagrán et al. (1999). (3) Mera and Lobos (2008). (4) Aigo com.pers. (5) Villagrán and Videla (2018). (6) Reyes et al. (2014). (7) Finkelstein (2006). (8) Kuschel et al. (1997). (9) Ramirez (1995). (10) Aigo and Ladio (2016). (11) Coña (2006). (12) Guevara (1908). (13) de Augusta (1916). (14) Koessler (2011)

[a] Ga: *Geotria australis* (Fam. Geotriidae)

[b] Lspp1, *Liolaemus* spp. (Fam. Iguanidae); Lspp2, *Liolaemus* spp. (Fam. Liolaemidae); Cp, *Callopistes palluma* (Fam. Teiidae); Tc, *Tachymenis chilensis* (Fam. Iguanidae)

[c] Pf, *Polypodium feuillei* (Fam. Polypodiaceae); Pe, *Pilea elliptica* (Fam. Urticaceae); Ca, *Centella asiática* (*Fam.* Apiaceae); *Jc*, *Juncus cyperoides* (Fam. Juncaceae); *Cs*, *Chloraea speciosa* (Fam. Orchidaceae); *St*, *Solanum tuberosum* (Fam. Solanaceae); *Cspp*, *Calceolaria* spp. (Fam. Calceolariaceae); *Gs*, *Greigia sphacelata* (Fam. Bromeliaceae)

perception of catastrophes and imbalances of the natural order. Villagrán and Videla (2018) point to this fact as especially interesting for Chile, where geological events such as volcano eruptions and earthquakes are frequent, highlighting both the ambivalence of the serpent symbol and the indifferentiation and metamorphosis between humans, animals, plants or geological formations. All these ideas make the concept of nature as a continuum within indigenous cosmologies (Aigo Personal Observation).

2.4 The Case of “Matuastos” in Patagonia

In Argentina, “matuastos” (“homeless” or “without a cave” in Quechua language) are species of lizards of the Leiosauridae family (Frost et al. 2001; Table 2.2), represented in Patagonia by the genera *Diplolaemus* (Bell 1843), *Pristidactylus*

Table 2.2 Bibliographic summary of the main features of species considered as “matuastos” from Patagonia based on Scolaro (2005, 2006) and Demangel (2016)

Species	Distribution in Patagonia	Biology	Habitat	Conservation status[a]
Diplolaemus sexcintus	Neuquén, Río Negro and Chubut (Argentina); Bío Bío and Araucanía (Chile)	Oviparous. Carnivorous (arthropods, invertebrates, juvenile *Liolaemus* and juvenile conspecifics). Active at cold temperatures. Aggressive. Can produce a high-pitched sound by violent expulsion of air	Patagonian steppe and ecotones with *Araucaria* and *Nothofagus* forests. Rocky outcrops, low shrubby areas	Least concern[1] Not threatened[2]
Diplolaemus darwinii	Chubut and Santa Cruz (Argentina); Magallanes (Chile)	Oviparous. Carnivorous (insects, juvenile lizards and conspecifics). Active at cold temperatures. Can produce a high-pitched sound by violent expulsion of air	Patagonian steppe. Areas with low vegetation cover of shrubs. Rocks and crevices	Least concern[1] Not threatened[2]
Diplolaemus bibronii	Chubut and Santa Cruz (Argentina); Aysen and Magallanes (Chile)	Oviparous. Carnivorous (insects, juvenile lizards and conspecifics). Active at cold temperatures. Can produce a high-pitched sound by violent expulsion of air	Patagonian steppe. Open areas with rocky soils, high shrubs and near sites with human presence	Least concern[1] Not threatened[2]
Diplolaemus leopardinus	Mendoza (Argentina)	Oviparous. Carnivorous (insects, juvenile lizards and conspecifics). Can produce a high-pitched sound by violent expulsion of air	Patagonian steppe and ecotones with *Araucaria* and *Nothofagus* forests. Rocky outcrops, low shrubby areas	Least concern[1] Vulnerable[2]
Pristidactylus araucanus	Mendoza and Neuquén (Argentina)	Oviparous. Insectivorous (ants and Coleoptera). Rare, more active at evening. Rock dwellers	Open Patagonian steppe and ecotones with Monte. Basaltic tablelands, rocky soils	Least concern[1] Vulnerable[2]
Pristidactylus fasciatus	Mendoza, Neuquén and Río Negro (Argentina)	Oviparous. Insectivorous (Coleoptera). Very agile and aggressive	Arid sands and scattered rocks of Monte shrubby steppes	Data Defficient[1] Data Defficient[2]
Pristidactylus nigroiugulus	Río Negro and Chubut (Argentina)	Oviparous. Carnivorous (other lizard species). Cave dweller	Rocky habitats of Patagonian steppe	Least concern[1] Not threatened[2]
Leiosaurus bellii	Mendoza, Neuquén, Río Negro, Chubut (Argentina)	Oviparous. Carnivorous and cannibal. Very aggressive. Crepuscular activity	Shrublands of Monte and ecotone Monte-Patagonian steppe. Sandy soils	Least concern[1] Not threatened[2]

[a] Conservation status: (1) *sensu* IUCN (2020); (2) *sensu* Abdala et al. (2012)

Fig. 2.2 Species of "matuastos" more common in north Patagonia: (**a**) *Pristidactylus nigroigulus* (Photograph by María Soledad Ausas), (**b**) *Leiosaurus belli* (Photograph by Fausto Méndez de la Cruz), (**c**) *Diplolaemus sexcintus* grey morph (Photograph by Nora Ibargüengoytía), (**d**) *Diplolaemus sexcintus* green morph (Photograph by Erika Kubisch)

(Fitzinger 1843) and *Leiosaurus* (Duméril and Bibron 1837). In some regions "matuasto" is also used to refer to the genus *Phymaturus* (Ibargüengoytía, personal communication) that is a member of the family Liolaemidae (Fig. 2.2). In this section we will explore the LEK on the "matuasto" through the compilation of ethnohistorical sources and preliminary field stories. One of the most widespread popular beliefs about reptiles in Patagonia refers to the presence of poison in "matuastos", but there is no evidence of the presence of venom glands in these lizards (Cei 1986, 1993). In this regard, a study carried out by Ibargüengoytía et al. (2005) analysed these local stories and its possible scientific explanation. In the cited work, a survey and the quantification of the oral microbiota of two "matuastos" of the genus *Diplolaemus* from Patagonia (*D. darwini* and *D. sexcintus*) was carried out in the laboratory. At least four known species of bacteria were present in the mouth of these lizards (*Staphylococcus warneri*, *Clostridium bifermentans*, *Clostridium perfringens* and *Stomatococcus mucilaginosus*; Ibargüengoytía et al. 2005). These species are known etiologic agents of a number of human and animal infections (Uzal et al. 1997; Uzal and Marcellino 2002). Therefore, the research has proven the existence of possible infectious agents, but according to the authors, these would not represent a mortal risk to humans or cattle (Ibargüengoytía et al. 2005).

Although there is little published about this group of lizards, some sources indicate that together with snakes, the "matuastos" might have played an important role in the cosmologies of the Mapuche and Tehuelche peoples (Alvarez 1992; Fernández 1995). Musters (1964) refers to the “matuasto” in the context of a trip he made with a group of Tehuelches from Punta Arenas to Carmen de Patagones. Referring to the matuasto he writes: …“Another animal which allegedly possesses magical powers is a flat lizard similar to a toad, which is believed to mysteriously make horses limp, and each time a horse encounters one, it dies…”. Similarly, Fernández (1995) in his book on Mapuche stories, refers to the “matuasto” and the viper as animals inhabited by the “wekufü” or evil spirits and used by the “kalku” or sorcerers, animals inhabiting the land below or “minche-mapu”, considered supernatural and malefic in the ordering of Mapuche cosmology. Moreover, Alvarez (1992) mentions a Mapuche story from Neuquén Province where the “matuasto” is described as… “a lizard with a stunted, aggressive and venomous tail, with the ability to jump; and once it has bitten you, it won’t let you go…”.

Fernández-Garay and Hernández (1999) refer to a conversation or Tehuelche story (a “nütram”, in its native tongue) about the “matuasto” (“kirke” or “k’amter”, according to Mapuche or Tehuelche language) as a variation of the origin of the fire myth, registered among the southern Tehuelches. This “nütram” is recounted by a member of the Mapuche-Tehuelche community “Manuel Quilchamal” (Southwestern Chubut Province, Río Senguer department) who mentions the “matuasto” as the former “fire owner or bearer”, a selfish ancestor who would not share the fire. Consequently, the “mara” or Patagonian hare (*Dolichotis patagonum*) took the fire from the “matuasto”. The lizard is portrayed as harmful and venomous: “they live out of the poison; the poison won’t let them die”. The emphasis falls on the use of fire that is essential to human survival, and therefore those who are not willing to share it are considered to be as hateful as the “matuasto”. According to Fernández-Garay and Hernández (1999) this account highlights the importance of an order necessary to human life and the danger of certain self-centred attitudes from those who are not willing to share their goods; the mythical fire bearer, the “matuasto”, is portrayed as an ancestor so different to people that it even mocks death being immortal, in stark contrast to the fragility of human life. Ethnohistorical information shows an agreement on regarding “matuastos” as immortal, malignant beings, poisonous and petty spirits. It is important, however, to understand some limitations of these collected stories and the need of interpreting them with caution. It is essential to take into account that these sources frequently hold a Western or Eurocentric view or interpretation of reality, where local popular knowledge is frequently tinted as superstition, myth or legend, in a contemptuous way (Caviglia 2011). Evidently, it is necessary to articulate the different sources, apart from deepening and producing new information about these lizards and other species of reptiles.

At present, there are recurring stories revolving around the “matuasto” in the Patagonian steppe. A research and extension project on reptiles developed by the authors in rural areas of Pichi Leufu, Pilcaniyeu and Cerro Alto in southern Río Negro Province[1] collected different stories among local communities about the

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[1] Scientific Extension/Divulgation Project: “The current and extinct reptiles of Patagonia, myths and legends: an exchange between the University and the Schools”. Ibargüengoytía N; Boretto J; Cabezas-Cartes F; Kubisch E; Duran F and Fernández M. Universidad Nacional del Comahue. CONICET.

"matuasto" and other reptiles. Sheepherders illustrate in their stories their concern for the effects caused by "matuasto" bites to their animals (dogs, sheep, horses) (unpublished data). They describe frequent biting events by "matuastos" on sheep during the lambing and lactation season (spring) mainly on the udders. These bites can allegedly cause a general weakening of the sheep and even death, mostly of females. Stories agree in pointing out the prolonged duration of the bite and the territorial behaviour of "matuastos", two known characteristics of this species. According to accounts, the sheep would approach the "matuasto" territory and despite the confrontation and warning by the lizard, they would not appear threatened and continue grazing; the lizard would then bite mainly the ears or the udders. The bitten animal would run, jump and buck to get rid of the lizard. After a few days the sheep would begin to weaken and could even die. The "matuastos", being territorial and aggressive species, do not flee before the presence of the sheep but face and warn them through vocalizations (Reyes-Olivares and Labra 2017). On the other hand, the periods of calving and lactation of the sheep may coincide with the time of egg laying of these lizard species, according to studies carried out on related species (midsummer, Migliore et al. 2017). Finally, in the same way, children from rural schools of these Patagonian locations tell stories about the warnings by their parents and grandparents against playing or crossing mallines, due to the presence of "matuastos" and to the perception of their dangerousness.

The type of conflict between inhabitants and "matuastos" herein reported resembles those observed in other works with reptiles (Alves et al. 2010) and those with other carnivores, such as puma in Patagonia (Llanos et al. 2016). In general, and as observed elsewhere (Marques 1995), the relationship between people and reptiles and especially with the "matuasto" that emerges in this preliminary analysis appears complex and laden by contradictions and ambiguities. It also points at the critical importance of deepening and strengthening the understanding of local views, attitudes and practices regarding reptiles to articulate meaningful education, management and conservation programs.

2.5 Conclusions

The information analysed in this chapter allows us to provide a general and first overview on the nature of the relationship between lizards and the people in Patagonia. Although scarce, the precedents on the human perceptions regarding reptiles give account on how different cultures can consider them either fascinating or scary. Particularly, the collection and analysis of ethnohistorical sources and preliminary field reports on the "matuasto" allow us to point out the cultural importance of this species, as well as the conflicting interaction with people. Based on these preliminary results we could say that the local perceptions on the "matuastos" as harmful and poisonous beings would provoke an attitude of unrest and rejection towards them. Although we point out the need for further studies, we emphasize the importance of knowing and pondering local visions, the intervening factors in their practices and the importance of integrating these with environmental education and effective management for the protection of the local herpetofauna.

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Part II
Land, Climate and Vegetation Background

Chapter 3
Geographical Singularities of the Patagonian Climate

Fernando Raúl Coronato

Abstract Patagonia (36°–56° S) is fully located in the belt of the southern hemisphere west winds, and because no other continental landmass stands in the way of the westerlies at these latitudes, the constancy and strength of these winds become decisive climatic factors. The westerly flow is fairly perpendicular to the Andean Range so as to create very sharp differences between both sides, mainly in precipitation. Thus, windward (Pacific side) mountainous wet Patagonia contrasts abruptly with leeward (Atlantic side) dry plateaus. This contrast is smoother northward, beyond the Patagonian limits, as the westerly flux slowly gives way to the subtropical anticyclonic prevalence. Because of this, both flanks of the Andes are equally dry north of parallel 32° S. Central Chile shows a clear Mediterranean climate, but the dry season shrinks dramatically south of 36° S until it disappears south of 40° S. Further south, on the Chilean flank of the Andes, the Patagonia climate clearly becomes an example of a cool temperate windward coastal area in midlatitudes. On the opposite side of the mountains, and because of their very presence, the climate of east Patagonia fits poorly in global classifications. Elsewhere on Earth, the eastern side of a continent at equivalent latitude would present a cool temperate climate, with a noted degree of continental and moderate rainfall. Instead, a windy rain-shadowed semidesert, strongly conditioned by the narrowness of the continent (<700 km) and the influence of the sub-Antarctic Ocean, spreads over extra-Andean Patagonia. The uniqueness of Patagonian current climate stems from large-scaled geographic factors that will be analyzed in this chapter.

Keywords Wind-conditioned climate · Westerlies · Southern midlatitudes · Rain shadow

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F. R. Coronato (✉)
Instituto Patagónico para el Estudio de los Ecosistemas Continentales – Consejo Nacional de Investigaciones Científicas y Técnicas (IPEEC-CONICET),
Puerto Madryn, Chubut, Argentina
e-mail: coronato@cenpat-conicet.gob.ar

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3.1 Study Area

The borders of Patagonia have always been very controversial. The very concept of Patagonia varies according to the disciplines. On the east the coasts of the Atlantic and those of the Pacific on the west do not pose any difficulty to delimit the region. To the south, there is an ambiguity with the Strait of Magellan, which separates Patagonia from Tierra del Fuego. Should this island be considered as the southernmost part of Patagonia, which would then culminate not in the Strait but in Cape Horn? However, it is in the north that the real difficulties to define the boundary arise.

Traditionally the Argentine geography considered a border as arbitrary as practical for all: the Colorado River, which crosses the Argentine territory entirely from the Chilean border to the Atlantic. This physical division has the great advantage of not breaking any of the five Argentine provinces located south of the river (Neuquén, Río Negro, Chubut, Santa Cruz, and Tierra del Fuego) and that are considered Patagonian. The small portion of the Province of Buenos Aires situated south of the Colorado is an individual administrative unit that does not lend itself to confusion insofar as it bears the name of Patagones.

However widespread or practiced, the frontier of the Colorado River could not sustain a more detailed, geographical, or ethnographical analysis. Indeed, from the point of view of physical geography there is a progressive transition between the plains of the Pampa and those of northern Patagonia. All that huge area is characterized by an extensive shrubland dominated by *Larrea* spp., interspersed with open forest of *Prosopis* spp., and belongs to the Monte phytogeographical region. In fact, the Monte biome is much more extensive spreading from the Chubut River (43° S) to Salta (25° S) (Abraham et al. 2009). Not only the Monte biome marks the continuity of Patagonian biophysical characteristics far beyond the Colorado River but also the Patagonian phytogeographical province itself, a colder biome that stretches over the plateaus and Andean foothills as north as 35° S in Mendoza.

On the other hand, west of the Andes, in Chile, it could be said that the northern border of Patagonia is even less defined than in Argentina. This is so perhaps because the very concept of Patagonia was born on the Atlantic coast in 1520, at the beginning to define the landscape of the arid plateaus along the shoreline. Thus, if all Chilean geographers agree that the arid plains along the Strait of Magellan are undoubtedly part of Patagonia, the conceptual disagreement begins as soon as one moves away from the interoceanic passage and the landscape becomes less flat and less arid. For some, the Chilean Patagonia does not go further north of the Taitao peninsula (47° S), which constituted a barrier for the circulation of the aboriginal coastal nomads; others take it to Reloncaví Sound (42° S), which carries the waters of the Pacific very close to the Argentine border. The extension of the concept of Patagonia to the north is a phenomenon that continues nowadays and that may stem on tourism marketing, nothing to do with biophysical or ethnographic features.

All in all, and in spite of the title of this chapter, the area to be analyzed from a climatological point of view exceeds the surface of Patagonia even in its widest acceptance. In order to meet the herpetology scope, this chapter will cover a broader area, well beyond Patagonian boundaries toward the north so as to include a great extent of Mendoza and La Pampa rangelands, in Argentina, and, very especially, an important area of central-southern Chile, perhaps the most favored of that country climatically speaking.

3.2 General Features

> In few parts of the world is the climate of the region and its life so determined by a single meteorological element, as is the climate of Patagonia by the constancy and strength of the wind (Prohaska 1976).

Patagonia, the southernmost region of the Americas, extends approximately from 36° S to 56° S; i.e., it is fully located in the belt of the west winds. Because of the triangular shape of the region, the continent is about 1500 km wide at the latitudes of north Patagonia and gradually narrows southward until it disappears in Cape Horn. Less than 1000 km separate it from the northernmost tip of the Antarctic Peninsula, but the Drake Passage is wide enough to sensibly warm the Antarctic air masses that may reach South America. In such a way, Patagonian winters are much milder than those at equivalent latitudes in North America. Although they are more frequent during the winter, maritime polar air masses can reach Patagonia throughout the year and they are one principal cause for the relatively low temperature in southern Patagonia (Weischet 1985).

In the South American quadrant the westerlies are put in motion by the interplay between the permanent subtropical anticyclones on the south Atlantic and southeast Pacific (both centered about on 30° S) and the subpolar low at 60° S (Prohaska 1976; Paruelo et al. 1998). The strong pressure gradient between the two belts generates the strong upper air westerly jet (Hobbs et al. 1998; Lenaerts et al. 2014); besides the seasonal N–S shift of the high cells is quite noticeably while the sub-Antarctic low belt hardly changes its position, thus in summer when the anticyclones move southward, the pressure gradient increases and consequently does wind speed too.

Since the main geographical feature of Patagonia, i.e., the Andean Range, intersects the dominant westerly flux perpendicularly, there is a very clear rain shadow effect eastward. This creates an abrupt contrast between windward, well-watered, and forested western Patagonia and leeward, namely, dry steppes covering plateaus and peneplains until the Atlantic shores. Even though the Andes south of 40° S seldom exceed 3000 m height, they generate abundant orographic precipitations over the Pacific flank. On the western side rainfall amounts may be up to 20 times greater than on the eastern flank, where in addition subsidence leads to arid and highly evaporative conditions downwind (Garreaud et al. 2013). This marked climatic contrast entails one of the sharper vegetation gradients in the world (Endlichter and Santana 1988; Warren and Sugden 1993).

In South America owing to the poleward movement of both subtropical anticyclones during the summer, anticyclonic influence is quite clear roughly until 40° S; thus, that season is usually sunnier and drier in the northern half of Patagonia (i.e., north 46° S). Because of this the climate of northwestern Patagonia could be considered as a type of an arid-degraded Mediterranean (Le Hoérou 2004). This area may be considered as a marginal area of the truly Mediterranean climate that predominates over central Chile. There, the weakening of the westerlies with decreasing latitude is reflected in the steady lengthening of the dry season, from none month at 40 °C up to all year round at 30 °C.

The Andean range between the latitudes 30–35° S is particularly high, with several summits over 6500 m. This explains that both sides of the mountains, although they share an insufficient rainfall amount, present different precipitation regimes. Whereas winter cyclonic rains prevail on the west flank foothills and the border of highest peaks, convective summer rains are the rule eastward over the Argentine plains. An incipient core of continentality develops on these rangelands east the Andes, and though annual temperature range is quite modest (17 °C), it is the greatest figure in the whole South America. This area is void of Pacific-originated moisture and, instead, the source of moisture is the distant Atlantic Ocean, at least 1000 km eastward. After gradually discharging its moisture on the pampas, the easterly winds reach the eastern foothills of the Andes with little water content and therefore the annual rainfall does not exceed 200 mm.

The only sporadic irruptions of Pacific air north of 35° S are the foehn events, locally known as “zonda,” which—accordingly to the strengthening of the westerlies—are more frequent during the winter.

The border between the air masses of the Pacific and those of the Atlantic roughly follows an oblique NW–SE line stretching from 35° S on the mountains to 41° S on the Atlantic coast. Southward, despite the fact that westerlies become dominant all the year round, some counteracting anticyclonic influence can be felt during the summer as already stated. Further east, on the Atlantic coast north of 46° S, summer drought may be slightly attenuated because of episodic ingressions of oceanic air masses from the Atlantic and consequent rainfall.

On the contrary, on both sides of the Andes south of 46° S the strong westerly flux is not counteracted at any season and thus rainfall is more evenly distributed throughout the year. Lesser seasonal variation of precipitation is not related to the total amount, which—as already said—decreases abruptly eastward the Andes.

Further south, beyond the 50° S parallel, cloudiness and precipitation are greater in summer according to the proximity of the subpolar regime, which in the southern hemisphere reaches much lower latitudes than in the north.

3.3 Wind Patterns

The average position of the front dividing South Pacific air masses from the SW and south Atlantic air masses from the NE depicts a NW–SE boundary, reaching the Atlantic coast at 41° S and fairly coincident with the Colorado River, i.e., the

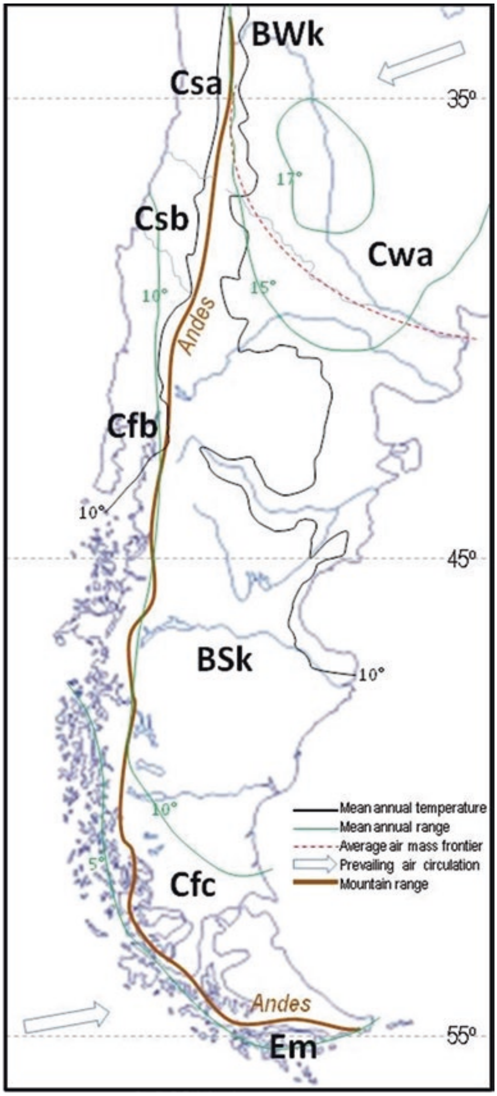

Fig. 3.1 Main features of Patagonian climates linked to Köppen climate classification system: *BWk* arid cool, *BSk* semiarid cool, *Csa* Mediterranean hot summer, *Csb* Mediterranean warm summer, *Cwa* dry-winter humid temperate, *Cfb* temperate oceanic, *Cfc* subpolar oceanic, *Em* subpolar oceanic no summer (Geiger 1954)

northern political border of Argentine Patagonia. South of this front, circulation from the west prevails, entailing the consequent strong W–E gradient of precipitation that characterizes the Patagonian climate. The prevalence of the westerlies provides a good criterion for the delimitation of Patagonia as a uniform climatic region (Fig. 3.1).

In all Patagonian stations west winds (i.e., SW + W + NW) count for 50–70% of all observations. Along the year some variations appear because of small seasonal displacements of the predominant pressure systems. In winter, due to the land mass cooling, a ridge over the continent connects the south Pacific and the south Atlantic anticyclones, located approximately at the same latitude and with similar intensities, and so isobars run parallel to latitudes resulting in a clear W–E component. On the contrary, in summer the two high-pressure cells are separated over the continent by a low-pressure trough, entailing a stronger (although never dominant) N–S component.

West of the Andes, in central Chile, prevailing wind is SW but strong local variations stem on the topography of the area, mainly on the barrier effect of the coastal range enhanced by quite compact mountain ranges between 35–37° S and 40–41° S. Thus, climate of the central valley flanked by the coastal range and the Andes is somehow more continental in those sectors, i.e., slightly drier, less windy, and warmer summers (31 °C, mean maximum January temperature in Talca, 35.43° S; the hottest summer in Chile).

Seasonal changes in high- and low-pressure centers not only affect wind direction but also control wind speed. This is especially true further south, in Patagonia, where the narrowness of the continent and the absence of another continental mass south of 40° S determine that general circulation patterns are simpler and more persistent than at equivalent latitudes in the Northern Hemisphere.

During the setting of summer, the subtropical south Pacific and south Atlantic anticyclones move a few degrees of latitude southward; on the other hand, the subpolar low-pressure belt has almost no displacement owing to the stability of underlying oceanic conditions. As result of this unequal displacement of the pressure belts, the barometric gradient between them strengthens as spring progresses (Lamb 1972). It stems on thermal differences between subtropical South America, which becomes warmer earlier, and the Antarctic sea ice, which persists still for 3 or 4 months more at 60° S (Burgos 1985). For this reason, although in Patagonia the average wind speed is quite high throughout the year, in most of the region it reaches the maximum in spring.

Strong winds play an important bioclimatic role because of the cooling effect and the systematic reduction of the temperature felt. Since—as said above—average wind speed is higher in the warm season, wind cooling effect is greater in this season too. This entails an apparent shrinking in the annual range of temperature and so climate is perceived as being cooler and more maritime than it actually is (Coronato 1993).

The effect of wind in reducing the boundary layer determines that the homeothermic animals must increase their energy investment to compensate for the additional heat loss. Ectothermic animals, and plants, also have a diminished ability to accumulate radiation and their temperature tends to equal that of air (Oke 1978). Weischet (1985) highlights the extent of this phenomenon in Patagonia, especially pernicious during the spring, supposed to be the blooming and reproductive season for most species.

3.4 Temperature Regime

Mean annual temperatures vary from 15 °C (7 °C in winter and 23 °C in summer) in north Patagonia to 5 °C (i.e., 0 °C in winter and 10 °C in summer) in Tierra del Fuego and southern Andes. Such differences are not surprising since, as already mentioned, Patagonia spans over 20° in latitude, i.e., about 2200 km in a N–S direction. In Europe, it would be the distance between Malta and Copenhagen (an equivalence not merely geometric but also environmental). Such latitudinal extension entails noticeable differences in the incoming solar radiation, which changes from little above 180 W/m^2 (annual average) in the northernmost stations, such as Neuquén or Curicó, to only 100 W/m^2 in Tierra del Fuego (Paruelo et al. 1998) or even less in the outermost islands of the Magellanic archipelago.

Due to the augmenting latitude the ratio summer/winter solar radiation increases progressively as well, from 4:1 at Neuquén (39° S) to 13:1 at Ushuaia (55° S). Nevertheless, the temperature regime follows an opposite pattern because of the narrowing of the continental mass southward; the mean annual temperature range varies from 16 °C in the north to 9 °C in the south or even down to 5 °C in the southern archipelagos that have been considered as having a "hyper-oceanic" climate (Tuhkanen 1992). In contrast, the northern value anticipates the already mentioned South American continentality core, centered around 35° S/66° W east to the Andes, while on the contiguous Chilean regions, because of the influence of the Pacific, annual temperature range does not exceed 12 °C (Fig. 3.1).

The extreme temperatures follow the same pattern, with maxima over 42 °C in north Patagonia and 38 °C as south as 46° S in eastern Patagonia; in turn, in Tierra del Fuego they do not surpass 30 °C and not even 20 °C in the hyper-oceanic islands. Further north, beyond the limits of Patagonia, extreme temperatures are very similar on both sides of the Andes; 45 °C was the highest temperature ever recorded in Mendoza city, in Argentina, as well as in Talca (Chile), previously mentioned as the warmest section of the Central Valley (35–37° S).

Excluding the high Andes, minima temperatures of −30 °C are recorded in the central tablelands as north as 41° S. Along the windward Pacific coast the absolute minima never go below −10 °C (Zamora and Santana 1979). Since maritime influence from the Atlantic does not penetrate much inland due to offshore circulation, temperatures below −10 °C are not rare in eastern Patagonia peneplains near the coast, though the shore itself is usually free of such values.

Besides the dramatic rainfall contrast produced by the Andean range, it is evident that the mountains restrict also the inland extent of maritime influences carried by the westerlies coming from the Pacific. However, it cannot be said that leeward Patagonia has a definite continental climate since annual temperature range is rather low (12 °C in average in eastern Patagonia). Indeed, authors disagree about qualifying the climate of the area within a continentality-oceanity continuum; whereas for Walter and Box (1983) it is "definitely maritime," for Mensching and Akhtar (1995) "it has distinct continental features." In fact, it is as if the continental characteristics generated eastward by the barrier of the Andes were attenuated by narrowness of the continent at these latitudes (Miller 1946), which obviously hinders the formation of continental air masses (Taljaard 1969).

3.4.1 Trends

Year to year variations of temperature are not in phase in the whole Patagonia; instead two main isofluctuative areas (N and S) were detected. These areas appear to be more dependent of latitude rather than affected by the Andean barrier, which in this matter behaves as a second-order differentiation factor. The meteorological stations that better correlated to each main area are Trelew and Río Gallegos, both located on the Atlantic coast at 43° S and 51° S, respectively (Coronato and Bisigato 1998).

Regarding long-term changes, a clear warming is noticeable in most of Patagonia since 1950 (Villalba et al. 2003; Vincent et al. 2005). On average, annual mean temperature increased 0.4 °C in the whole region; also a decline in the number of cold days and an augmentation of warm days since 1960 was reported (Rusticucci and Barrucand 2004).

3.4.2 Wind Chill

Treating wind and temperature separately as done above fails in reflecting accurately the climatological weight these factors have when acting simultaneously as always happens in real conditions. We briefly mentioned this topic when referred to the effect of wind in reducing the boundary layer; yet in Patagonia the wind cooling effect deserves further attention since it is a major bioclimatological issue. The first permanent European settlers in the mid-nineteenth century soon became aware of this climatic constraint: “certainly it is not a very low temperature compared to those of Canada, but when these low temperatures are coupled with a strong wind, as it occurs often in Chubut, cold is almost insupportable” (Hughes 1927).

Since in Patagonia east of the Andes wind speed is higher in summer (as it can be seen in Table 3.1), the wind cooling effect is also greater in this season (4.7 °C versus 3.6 °C) (Coronato 1993). Thus, the climate of the plains is perceived not only as being cooler than it is but also more maritime because of the diminished annual thermal range of equivalent temperatures (eT). The opposite occurs west of the Andes, especially on the Pacific shoreline openly exposed to the west winds; as their speed increases during the winter, they therefore determine an overcooling in that season. However, being that the actual temperatures are not too low (once again because of the maritime influence), eT remain higher than the ones experienced east of the mountain range.

The eT pattern of two contrasting locations of eastern Patagonia, Puerto Madryn (42.7° S, 65° W) and Punta Arenas (53.1° S, 71° W), is shown by means of the

Table 3.1 Seasonal and geographical wind speed variation

Mean wind speed (m/s) at 1.5 m above ground level				
Average of nine east coast, seven inland, and three west coast sites (series 1978–1985)				
Area	Summer	Winter	Year	Variation (%)
East coast	4.6	4.1	4.3	12
Inland	4.1	2.8	3.5	46
West coast	4.3	4.0	4.2	8
Whole region	4.3	3.6	4.0	20

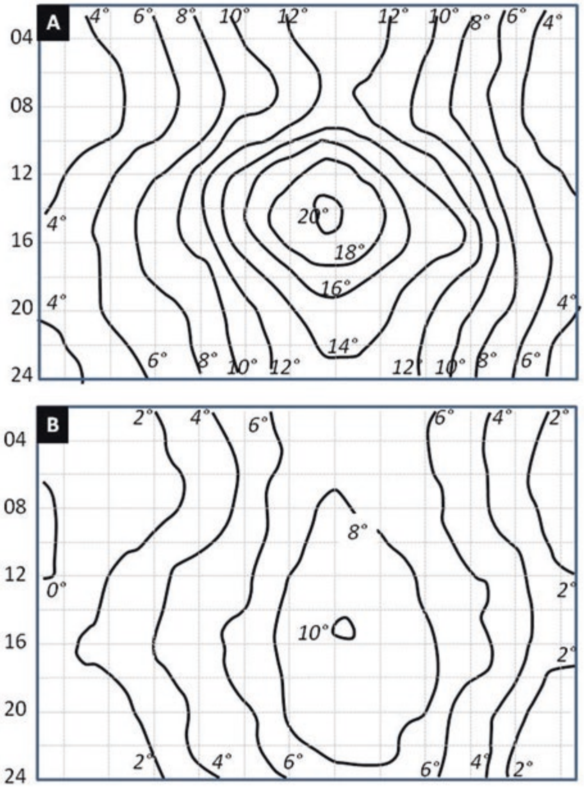

Fig. 3.2 Diurnal × monthly equivalent temperatures; (**a**) Puerto Madryn, (**b**) Punta Arenas (hours of the day on *y*-axis; months of the year on *x*-axis)

diurnal × monthly isopleth diagrams of average hourly eT (Fig. 3.2). They allow to compare the result of wind cooling on the thermal regime along the year. Both stations are quite separated in latitude so as to include most of Patagonia between them; both are at the sea level and mean annual temperatures are 14 °C and 7 °C, respectively, while mean annual wind speed are 2.4 m/s and 3.7 m/s.[1] Those figures

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[1] Taken from Coronato (1995) and Endlichter and Santana (1988), respectively.

determine an annual average eT of 10 °C in Puerto Madryn and 3 °C in Punta Arenas, corresponding roughly to a heat loss (HL) of 590 W/m^2 to the former and 780 W/m^2 to the latter.

In the isopleth diagrams of Fig. 3.2, the number of intersections of the contour lines with an imposed 12 × 12 grid is a measure of the trends of eT fluctuations according to S (seasonality; horizontal gridlines, i.e., variation along the year) or D (diurnality; vertical gridlines, i.e., variation along the day). It can be seen that both parameters are greater in Puerto Madryn according to the higher continentality in the north; also, in agreement with midlatitudes it is clear that $S > D$ in both locations. Wind cooling effect is evidenced by the flattening of the eT daily curve when compared to actual temperature. Whereas in midsummer (January) the daily range of temperature is 14 °C in Puerto Madryn and 8 °C in Punta Arenas, the range of eT lessens to 6 °C and 4 °C (Fig. 3.2a, b, respectively).

Figure 3.3 shows 31 Patagonian weather stations ordered by mean annual temperature and wind speed; thus, more severe eT conditions are in the bottom right corner whereas less severe are in the upper left corner. It can be seen that most of Patagonia falls within the eT range of the two analyzed locations (n°23 and 26), materialized by the oblique dashed lines. Several inland localities situated well above sea level, in which mean actual temperature may be lower because of elevation, do not experience eT values lower than coastal stations since wind speed in lower inland (see Table 3.1) and thus wind cooling effect is less marked. This turns out in more even equivalent temperatures between coast and inland.

In short, the bioclimatic effect of wind cooling could be summarized by marking the fact that wind smoothes thermic differences between coastal and interior regions, as well as along the day or along the year.

3.5 Precipitation and Moisture Budget

The barrier to the westerly winds that form the Andes has already been mentioned as the main geographic factor affecting the climate of South America south of 35° S. The rain shadow effect increases as the prevalence of the westerlies and the rainfall they bring increase as well. North of parallel 32° S both flanks of the Andes are equally dry but noticeable differences appear southward and become marked south of 35° S. From that latitude on, differences in precipitation at both sides of the barrier reaching a 10:1 ratio within a distance of 150 km are far from uncommon and may even reach 20:1. The sharpest rainfall gradients are coincident with the highest sectors of the mountain range (48°–51° S) that enhance the contrast between uplift-induced hyper humid conditions on the west side and stronger leeward subsidence evaporative conditions (Garreaud et al. 2013). Annual precipitation in such windward areas may surpass 6000 mm (Miller 1946) yet an average rainfall amount throughout the west flank of the Andes may be figured around 2000 mm. Only north of parallel 37° S, where westerlies begin to weaken, yearly rainfall goes down 1000 mm on the Chilean side. The transition between wet southern Chile and the

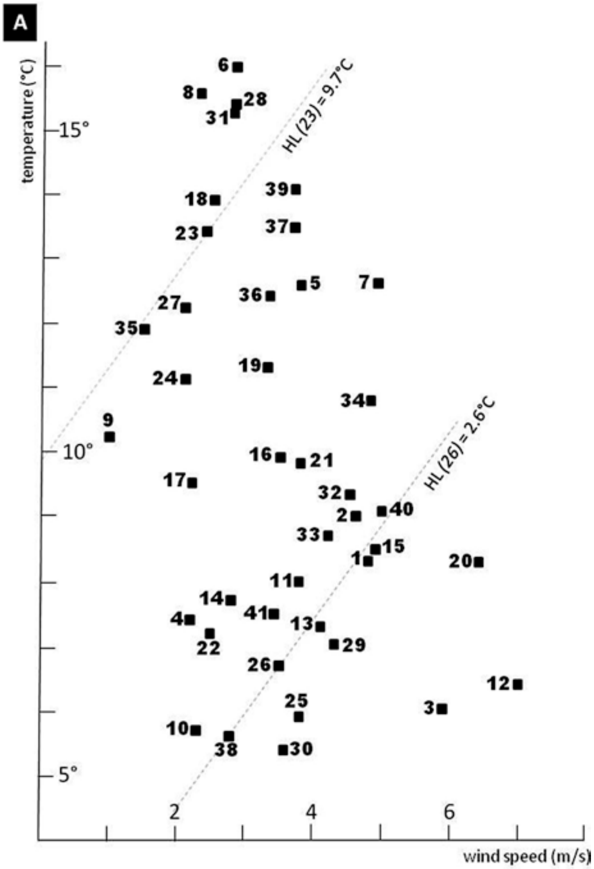

Fig. 3.3 Patagonian stations ordered by average annual temperature and wind speed Weather stations whose temperature and wind mean annual values are graphed: (*1*) Bariloche, (*2*) Cabo Raper, (*3*) Cabo Vírgenes, (*4*) Calafate, (*5*) Camarones, (*6*) Choele Choel, (*7*) Comodoro Rivadavia, (*8*) Conesa, (*9*) El Bolsón, (*10*) El Turbio, (*11*) Esquel, (*12*) Evangelistas, (*13*) Fitz Roy, (*14*) Gobernador Costa, (*15*) Gobernador Gregores, (*16*) Las Heras, (*17*) Maquinchao, (*18*) Neuquén, (*19*) Paso de Indios, (*20*) Perito Moreno, (*21*) Puerto Deseado, (*22*) Puerto Edén, (*23*) Puerto Madryn, (*24*) Puerto Montt, (*25*) Puerto Stanley, (*26*) Punta Arenas, (*27*) Punta Delgada, (*28*) Río Colorado, (*29*) Río Gallegos, (*30*) Río Grande, (*31*) San Antonio, (*32*) San Julián, (*33*) Santa Cruz, (*34*) Sarmiento, (*35*) Sierra Colorada, (*36*) Temuco, (*37*) Trelew, (*38*) Ushuaia, (*39*) Viedma, (*40*) Zapala, (*41*) Coihaique

desert covering the northern third of the country is very clearly evidenced by the number of dry months, i.e., those in which the precipitation (in mm) is less than twice the temperature (in °C). There is just one dry month at 39° S, 3 months at 37° S, 5 months at 35° S, 7 months in Santiago at 33° S, and all the year round beyond La Serena at 30° S.

Everywhere on the Patagonian plateaus in the Argentinean side, average yearly rainfall is about 200 mm, and even some spots with less than 150 mm are recorded as near as 150 km from the Pacific shores (Smith and Evans 2007). The result is a very marked vegetation gradient that starts on the Pacific coast with a wet temperate forest, turns into Alpine forests and grasslands, and changes again into moderate continental forests to merge finally into arid rangelands stretching over hundreds of kilometers until the Atlantic (Bailey 1989). It is possible to seize this vegetation gradient in the glacial lakes of the Argentinean side while standing at the distal eastern end, in pebbled wide beaches on morainic hills, surrounded by xerophytes and active sand dunes, looking west toward the Andean section of the lake, where long sounds deeply penetrate between snow-capped mountains, covered by a humid and cool forest.

If precipitation amounts change sharply at both sides of the Andes south of 35° S parallel, rainfall seasonality, cloudiness, and temperature regime do not or much less marked. The mountain range does not affect the cloudiness and temperature regimes as it affects precipitation. The annual isonephs of sky cover show a roughly latitudinal pattern ranging from 50% in north Patagonia to 70% in the south, with a noticeable inward depression (Prohaska 1976). Although percentages of sky cover are quite similar at both sides of the mountains, the type of cloudiness is not the same. Very often, mid and high cloudiness in eastern Patagonia (as far as the Atlantic coast) is merely residual cloudiness generated by the orographic uplift of the wet Pacific air over the Andes.

In the whole Patagonia north of the 50° S parallel most of precipitation falls from May to October (46% during the 3 winter months, i.e., June to August) (Labraga and Villalba 2009; Jobbágy et al. 1995). This seasonality stems on the equatorward shift of the westerlies, which increment the frequency of front activity coming from the Pacific (Garreaud and Aceituno 2007). Even if rainfall amount is low, the fact that the winter is the rainy season in north Patagonia east of the Andes, it is a Mediterranean-like feature that this region shares with the Mediterranean core of central Chile. Eastward, where some influence of Atlantic air masses becomes noticeable especially in summer, precipitations are more evenly distributed throughout the year (Jobbágy et al. 1995). In fact, in eastern Chubut there is not a defined rainy season and toward the northern portions of the region (east of Río Negro), the rising of summer rainfall anticipates the subtropical continental pattern of central and northern Argentina and it affects most of the Monte biome. South of 50° S, and on the Pacific coast south of 47° S, a summer rainfall pattern is recorded; it is a subpolar maritime pattern conditioned by the sea temperature, located in latitudes as low as nowhere else in the world.

3.5.1 Trends

Unlike what happens with temperature, precipitation did not show significant changes in the last 50 years in most of Patagonia; besides, year-to-year variability overrides long-term changes throughout the region. Nevertheless, different models agree in forecasting 10% less rainfall within the near future scenarios, mainly in northern Patagonian Andes (Masiokas et al. 2008). In agreement to this and in the conterminous central Chile, a decrease greater than 20% was recorded during the last century (González et al. 2011) and further decreasing up to 40% of summer rainfall is foreseen along the present century (CONAMA 2006).

As the major rivers of Eastern Patagonia have their headwaters in the Andes, north of 45° S (i.e., Colorado, Neuquén, Limay, Chubut, Senguerr), and that most of Patagonian population depends exclusively on water carried by these streams, any reduction of rainfall is not to be neglected, above all because it is linked to foreseen higher temperatures, i.e., greater atmospheric demand.

3.5.2 Water Balance

It was already seen how wind alters the bioclimatic role of temperature in Patagonia. Indeed, wind also alters the water balance by dramatically increasing evaporation. Whether the ratio between monthly evaporation rates and monthly mean temperatures is about 5–7 in wetter and less windy climates of Argentina, it reaches 10–15 in eastern Patagonia because of higher wind speed (Walter and Box 1983). Moreover, once the onshore westerlies dropped their humidity on the windward flank of the Andes and cross the mountains downward, their evaporative power is enhanced because of the adiabatic heating, making that atmospheric demand be as high as 1200–1400 mm/year in central Patagonia. The strong negative water balance affects the whole extra-Andean region; only on the west side of the mountain range the water balance becomes positive.

Notwithstanding, due to the increasing of precipitation during the winter, water balance in some eastern areas may be positive during the rainy season. Obviously, the length of the positive balance situation diminishes eastward, ranging from 5 months on the Andean foothills (Bariloche, May–September) to none on the Atlantic shore of Chubut or northern Santa Cruz.

The aridity index (IA) defined as the ratio between mean annual precipitation and potential evapotranspiration (Le Hoérou 2004)[2] is very clear in defining driest areas of Patagonia (Fig. 3.4). It can be seen that Patagonia is split in two contrasting areas from a hygric point of view and it is worthy to note that transitional areas (SA and SH) are confined to two narrow fringes over the east Andes foothills and only expand toward the south, in the Magellan area.

3.6 Climatic Classification

From everything explained up to this point it emerges that eastern Patagonia fits badly in a global climatic classification. There is nowhere else in the world an arid region on the eastern side of a continent in midlatitudes. Elsewhere, a region so

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[2] HA = HyperArid (IA < 0.05); A = Arid ($0.05 <$ IA < 0.2); SA = SemiArid ($0.2 <$ IA < 0.5); SH=SubHumid ($0.5 <$ IA < 0.75); H=Humid (IA > 0.75).

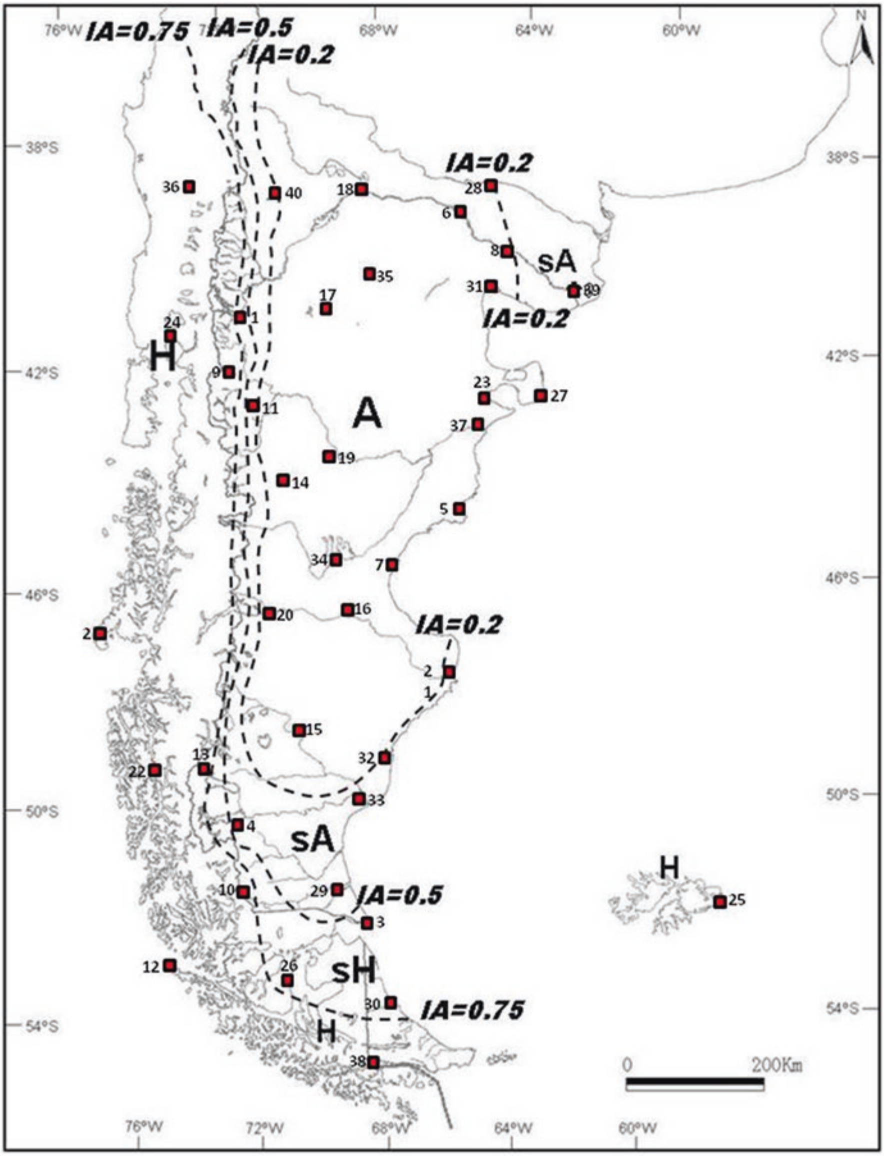

Fig. 3.4 Aridity index in Patagonia (see footnote 1)

located would present a cold temperate climate, rather continental and with a moderate annual rainfall amount (a Cfb or Dfb climate in Köppen's classification). Instead, eastern Patagonia exhibits a temperate dry climate with moderate annual temperature range; that is, a BSk climate or even a BWk in drier areas. The same arid climates span beyond the northern border of Patagonia, on the plains of

Mendoza and eastern Andean foothills, and cover—or indeed define—the Monte Desert biome, stretching up to 25° S and connecting to the South American Arid Diagonal, of which—in fact—Patagonian steppe is the southernmost link.

The uniqueness of rain-shadowed east Patagonian climate is reinforced by the sharp contrast with western Patagonia, which displays an oceanic climate (Cfc) a little colder than its counterparts elsewhere in the world, especially because of the lack of real summer heat (Weischet 1985). North of the 37° S parallel, where a dry period begins to appear during summertime, the Cf climate gives way to Cs climate, Csb first and Csa further north as summer becomes hotter. This is the core of the Mediterranean climate of central Chile (Fig. 3.1).

North of the 51° S parallel the Cfc climate is restricted to the Pacific coast and the west flank of the Andes but further south it stretches all across the continent until the Atlantic coast so as to include the Falkland Islands as well. The southernmost areas of Tierra del Fuego, where summer mean temperature does not surpass 10 °C, have thus an Em climate clearly marked by the lack of heat.

On the opposite end, as it can be seen on Fig. 3.3 north of 40° S, where westerlies fail, a less arid area appears eastward owing to the last regular rainfalls originated in the Atlantic Ocean. In this semiarid area, as rainfall increases northward the BSk climate tends toward a subhumid Cwa climate with some continental features. According to the flat topography, climatic transition is extremely gradual, so the northern border of Patagonia is really ill-defined on earth as in sky.

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Chapter 4
Landscapes and Geology of Patagonia: An Introduction to the Land of Reptiles

Pablo José Bouza and Andrés Bilmes

Abstract The purpose of this chapter is to summarize the geological-geomorphological regions of Patagonia with a general characterization of the main geomorphological units. A review of studies on geology, stratigraphic, main geologic landmarks, geological history, and geological resources will be briefly described. This review was performed on the base of geological province concept, including a stratigraphic-morphostructural criteria and a description of major endogenous and exogenous processes responsible for the formation of landscape units. In this chapter these geological-geomorphological regions include Chile and Argentina and were grouped as: (1) Coastal Cordillera and Central Valley (Chile), (2) Southern Andes Cordillera, (3) Mountain Sector of the Neuquén Embayment, (4) Northern Patagonian Tablelands, (5) The North Patagonian Broken Foreland and Somún Curá Massif, (6) Central Patagonian Tablelands, (7) Deseado Massif, (8) Southern Patagonian Tableland, and (9) Islas Malvinas Plateau.

Keywords Patagonian Andes · Extra-Andean Patagonia · Geological provinces · Geomorphological processes

4.1 Introduction

The region considered in this chapter occupies more than 1,000,000 km^2 and is the only continental landmass emerging along the midlatitudes in the Southern Hemisphere (Fig. 4.1). The region involves two different countries, Chile to the

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P. J. Bouza (✉)
Instituto Patagónico para el Estudio de los Ecosistemas Continentales – Consejo Nacional de Investigaciones Científicas y Técnicas (IPEEC-CONICET),
Puerto Madryn, Chubut, Argentina
e-mail: bouza@cenpat-conicet.gob.ar

A. Bilmes
Instituto Patagónico de Geología y Paleontología – Consejo Nacional de Investigaciones Científicas y Técnicas (IPGP-CONICET), Puerto Madryn, Chubut, Argentina
e-mail: abilmes@cenpat-conicet.gob.ar

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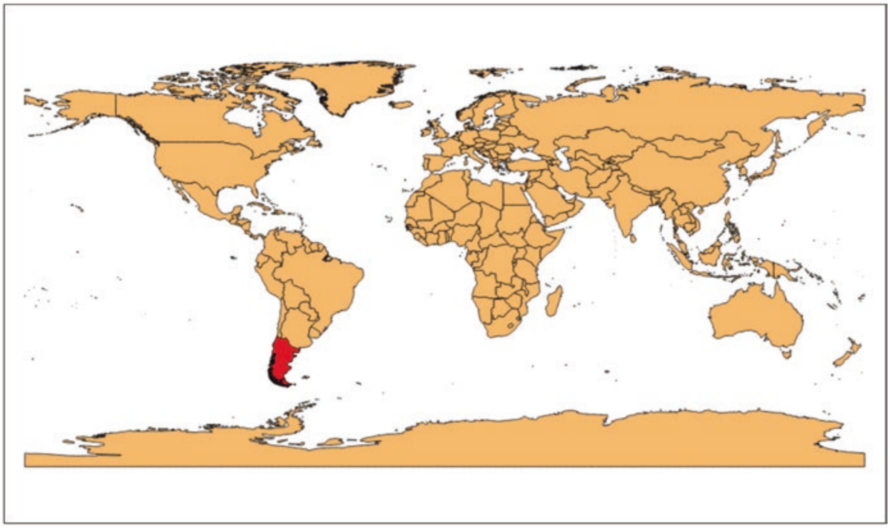

Fig. 4.1 Patagonian region emerging along the midlatitudes in the Southern Hemisphere

west and Argentina to the east. Its natural boundaries are from the north of the Barrancas and the Colorado Rivers in Argentina (Provinces of Mendoza and La Pampa and the southern portion of Buenos Aires) and by the Maule River in Chile. To the south, the natural boundaries are the Cabo de Hornos (Cape Horn), the Canal de Beagle, and the Navarino Island archipelago (Fig. 4.2).

While it is generally accepted that the beginning of the Andean margin configuration is determined by the start of the subduction at the western margin of the South American plate at around 190 Ma (D'Elia et al. 2012), the main configuration and development of the Andes and Andean Foreland was developed during the Neogene (18 Ma; Folguera and Ramos 2011; Bilmes et al. 2013, 2017a). At this time a renewed episode of orogenic grow started and shifted toward the foreland during the lower to upper middle Miocene (19–10 Ma; Guillaume et al. 2009; Bilmes et al. 2013). In addition, since the Late Miocene-Pliocene the foreland region is characterized by a regional uplift, a process that is still observed today (Guillaume et al. 2009; Pedoja et al. 2011; Folguera et al. 2015). As a consequence of this foreland uplift several Late Miocene-Pliocene fluvial terraces were tilted and all Pleistocene Atlantic shorelines were remarkably elevated, in some cases more than 100 m with respect to present-day sea level (Pedoja et al. 2011).

At the western side of the Patagonian Andes, the wet west winds produced a rain shadow; therefore the western slope of the Patagonian Andes was subjected to an extreme erosional gradient producing asymmetric erosion with respect to the eastern slope. The end of early Miocene period is marked by an increased aridity of the eastern side of Patagonian Andes (Bellosi 1999; Blisniuk et al. 2005; Palazzesi et al. 2014; Bucher et al. 2018). Due to this change on climatic conditions, from the physiographic point of view, two contrasting sectors can be distinguished: (1) the

Fig. 4.2 Patagonian geological-geomorphological regions (Modified from Ramos 1999; Coronato et al. 2008) and major geological structure features

Patagonian Andes (North and South Patagonian Cordillera and Fueguian Andes; Ramos 1999) and (2) the Extra-Andean Patagonia, which extends eastward up to the Atlantic Ocean.

Glaciation processes mainly modeled the landscape in Patagonian Andes. The mountain range was covered by a continuous mountain ice sheet (continental and alpine-type glaciations), from 37° S to 56° S (Cape Horn), during at least five major glaciations over the last million years, beginning with the Great Patagonian Glaciation (GPG) (Fig. 4.3; Rabassa and Clapperton 1990; Rabassa 2008; Caldenius 1932; Bendle et al. 2017; Griffing 2018). The landscape of the Extra-Andean Patagonia region is modeled by severe aridity conditions (low rainfall rate and

Fig. 4.3 Late Glacial Maximum (LGM) and Great Patagonia Glaciation (GPG) in Patagonia (Modified from Caldenius 1932; Bendle et al. 2017; Griffing 2018). NPI North Patagonian Icefield, SPI South Patagonian Icefield, CDI Cordillera Darwin Icefield

sparse vegetation cover) with major influence in the operation and development of landforms (Thomas 1997).

Although wind is an important geomorphological agent that has deeply modified the arid regional landscapes, water erosion due to short- and high-intensity rainfalls is the most active exogenous geomorphic process, either as raindrop splash, as surface runoff, or as concentrated flow erosion, in the form of rills and gullies. Many of these landforms exhibit large patches of bare soils (desert pavements and surface soil crusts) and thus they are exposed to wind erosion, raindrop impact, and surface runoff (Bouza et al. 1993; Bouza and del Valle 1997; Rostagno and Degorgue 2011; Chartier et al. 2013).

The main feature of Extra-Andean Patagonia is the presence of extensive plains of different origins and ages, placed at different levels. This relief is occasionally interrupted by the appearance of rocky cliffs, lava plains (plateaus), and low mountain hills. In the southern sector the major landforms are of glacial origin: great moraines produced during several glaciations, mainly during the Last Glacial Maximum (LGM, ca. 24 ka; Fig. 4.3).

From a geologic point of view, Patagonia can be divided into geological provinces. The term geological province refers to a region characterized by a certain stratigraphic succession, its own structural style, and peculiar geomorphological features, being the whole expression of a particular geological history (Rolleri 1976; Ramos 1999). This morphostructural criterion is useful to describe the landscape units associated to the main endogenous and exogenous processes.

In this chapter, nine geological-geomorphological regions are described to characterize the general Patagonian landscape. The definition and delimitation of the units adopted in this work follows, with some modifications, the proposal of Ramos (1999) and Coronato et al. (2008) (Fig. 4.2).

4.2 Coastal Cordillera and Central Valley

The Costal Cordillera and the Central Valley are two geological regions completely developed in Chile (Fig. 4.2). The Coastal Cordillera is a coastal batholith (between 18° and 42° S) directly on the Pacific shoreline formed by predominately Late Paleozoic and Mesozoic igneous rocks, with parallel belts of Paleozoic metamorphic rocks outcropping out south of 34° S. It is the oldest and westernmost remnant of a magmatic arc formed during the birth of the modern Andes (195–130 Ma). With a moderate height, about 1000–2000 m a.s.l., it disappears completely in Northern Chile near Arica (Pankhurst and Hervé 2007; Casanova et al. 2013). Only the southern extremity of this range concerns the study region.

In the Patagonia region, this geological province is mainly represented by the Bahía Mansa Metamorphic Complex of Carboniferous and Permian-Triassic ages, outcropping between 39° 30′ and 42° 00′ S. This Metamorphic Complex corresponds to a heterogeneous group of metamorphic rocks, with mainly pelitic to semipelitic schists, which are well exposed in the coastal cliffs (e.g., Valdivia; Fig. 4.4a, b). Further south, in the island of Chiloé, Paleogene volcano and sedimentary rocks are outcropped (Duhart et al. 2001).

The Central Valley is located between the Andes to the east and the Coastal Cordillera to the west and thus it runs along a north-to-south axis adjacent to the southeastern Pacific shoreline (Fig. 4.2). The area includes the Chilean Lake District and the Chilotan archipelago, most noteworthy Isla Grande de Chiloé (between 40°

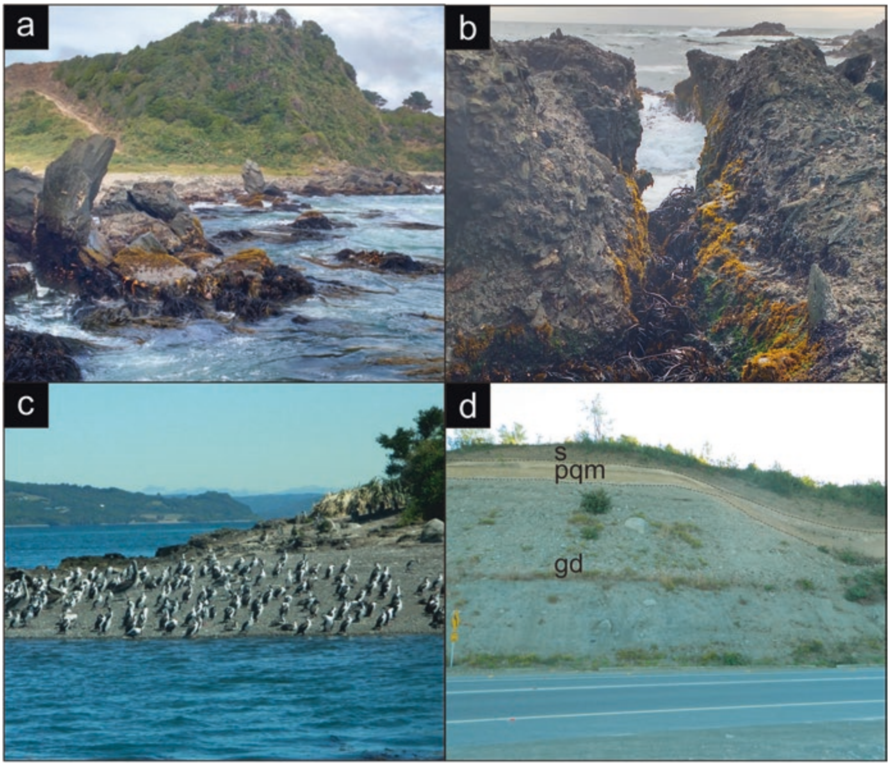

Fig. 4.4 Coastal Cordillera and Central Valley; (**a**, **b**) metamorphic rocks in coastal cliff (**c**) Chilotan archipelago; (**d**) LGM Llanquihue glaciation, gd glacial deposit, pqm pyroclastic Quaternary materials, s soil

and 44° S; Fig. 4.4c). The valley floor features large lakes and marine water bodies that were filled during the Last Glacial Maximum (LGM, Llanquihue glaciation) by Andean piedmont ice lobes. The rest of the valley floor is covered with moraine belts and outwash plains deposited by those lobes during both the LGM and earlier glacial expansions (Andersen et al. 1999; Moreno et al. 2015). In sectors, the glacial substrate was covered by pyroclastic materials, derived from Quaternary volcanoes, on which soil developed (Fig. 4.4d; Casanova et al. 2013).

4.3 Southern Andes Cordillera

This region includes four geological provinces defined by Ramos (1999): (1) the southern portion of the Cordillera Principal (between 34° and 39° S), (2) the Cordillera Patagónica Septentrional, (3) the Cordillera Patagónica Austral, and (4) the Cordillera Fueguina (Fig. 4.2).

These geological provinces have been considered as a whole because of the common mountainous and glacial landscape and similar physiographic features. The mountainous landscape of Southern Andes Cordillera is distinguished according to the type of endogenous geological processes produced northward or southward from the triple junction tectonic plates (Fig. 4.2). The associated geomorphic elements to volcanoes in Patagonian Andes are volcanic scum, lava tunnels, lava flows, and volcanic boiler calderas.

The southern part of the Cordillera Principal and the Cordillera Patagónica Septentrional (Ramos 1999) are characterized by mountain peaks associated with igneous rocks of the Patagonian Batholith (González Díaz 1982; Rapela et al. 1987) and with Neogene-Quaternary stratovolcanoes; some of them are active or potentially active, which indicates the Southern Volcanic Zone (SVZ, 33–46° S). The SVZ includes at least 60 volcanoes in Chile and Argentina, as well as three caldera systems and numerous minor eruptive centers (Stern 2004; Moreno et al. 2015) (Fig. 4.5a, b; e.g., Lanín, Osorno, Villarrica, Cordon Caulle-Puyehue, Hudson, and Quizapú, among others), being some of them very active in the past decade (e.g., Cerro Hudson eruption in August 1991, Volcán Chaiten eruption in February 2009, Cordón Caulle-Puyehue eruption in June 2011, Volcán Copahue eruption in December 2012, Volcán Calbuco eruption in April 2015) Petrinovic and D'Elia 2018.

The Cordillera Patagónica Austral (Leanza 1972) is characterized by two sectors: (1) a gap of inactive volcanism that occurs between 46° and 49° S and (2) another volcanic area that appears southward of the Austral Volcanic Zone (AVZ; 49–55° S). The Cordillera Patagónica Austral (mostly within the gap of inactive volcanism) includes peaks composed of isolated plutons of the Patagonian Batholith, like Cerro San Valentín, Cerro San Lorenzo, Cerro Fitz Roy (Chaltén; Fig. 4.5c), Cerro Poincenot, Cerro Torre, and Torres del Paine granitic intrusions of Early Miocene age (Skarmeta and Castelli 1997; Ramos and Ghiglione 2008). These peaks do not correspond to volcanic bodies and with the exception of Cerro San Lorenzo, these igneous intrusives (stocks) were emplaced on Cretaceous marine sedimentary rocks belonging to the Austral (or Magallanes) Basin. The Cerro San Valentín (4070 m a.s.l.) is the highest peak in the Patagonian Andes and is just south of the Chile Ridge. This significant change in elevation north and south of 46°30′ S latitude coincides with the collision of the Chile Ridge (Ramos and Ghiglione 2008). The Austral Volcanic Zone (AVZ; 49–55°S) consists of five stratovolcanoes and a small complex of Holocene domes and flows on the Cook Island, the southernmost volcanic center in the Andes south of the Magallanes fault zone and therefore on the Scotia Plate (Fig. 4.2).

The Cordillera Fueguina (Borrello 1972) is represented by a mountain range located in the southern sector of the Isla Grande de Tierra del Fuego. This is the only Andean segment that extends in a W-E direction, from the Magellan fault, in the South Pacific Ocean, to the Isla de Los Estados (Staten Island), in the South Atlantic Ocean. It includes the lowest Andean summits of Patagonia: in Chile region, the Monte Sarmiento in Darwin Cordillera reaches 2488 m a.s.l., while in Argentina, the Monte Olivia and the Monte Cornú do not exceed 1500 m a.s.l. According to Coronato et al. (2008), Cordillera Fueguina is characterized by three areas: (a) the Fueguian Archipelago, in the western and southern Chilean sector, formed by plutonic rocks resulting from several intrusions during the Cretaceous and the Cenozoic,

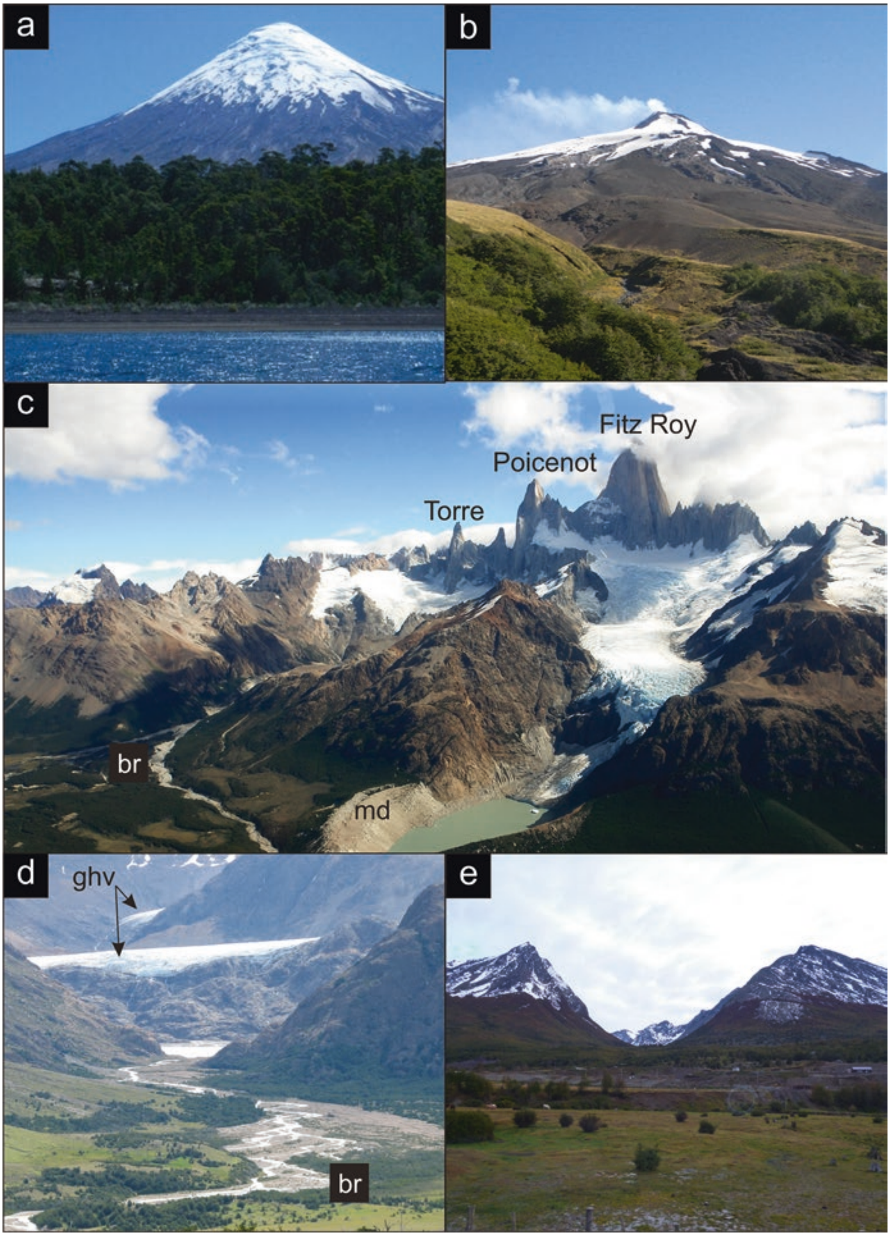

Fig. 4.5 Southern Andes Cordillera; (**a**, **b**) Southern Volcanic Zone, Osorno and Villarrica volcanoes, respectively; (**c**) gap of inactive volcanism, Cerro Fitz Roy, Cerro Poincenot, Cerro Torre (courtesy of photographer Daniel Rivademar), moraine deposits (md) from LIA (glacial retreat), braided rivers (br); (**d**) valley of glacial origin (Río Tunel, Chalten), in the background, a hanging glacier is observed (ghv, Tunel Inferior Glacier); (**e**) U-shaped valleys (Ushuaia, Tierra del Fuego)

(b) the Fueguian Cordillera, and (c) the foothills of the Fueguian Cordillera, north of Lago Fagnano, up to 53° 30′ S, approximately.

Since the Late Miocene (ca. 6 Ma), glaciations were the main geomorphic processes that modeled the landscape of the Southern Andes Cordillera (Fig. 4.3). The present drainage network was developed after the Last Glacial Maximum (LGM) since ca. 21 ka BP. Figure 4.3 shows the maximum advance of the GPG and the LGM, respectively. Presently, tree icefield relicts are recognized: North Patagonian Icefield, South Patagonian Icefield (Hielo Continental Patagónico, Norte y Sur, respectively), and Cordillera Darwin Icefield.

The landscape in the Southern Andes Cordillera is mainly characterized by abrasion action during glacier advances. The resulting erosional landforms include striations, cirques, arêtes, nunataks, glacial horns, U-shaped valleys, and hanging valleys (Fig. 4.5c, d, e). Nunataks are mountainous peaks resulting from the residual relief that resisted the alpine glacial erosion, emerging as a relief in the form of islands, similar to inselbergs or witness hills. These landforms concern hypothetical glacial refuges during glacial periods. For example, Fitz Roy (or Cerro Chaltén, 3405 m a.s.l.), Poincenot, Torre, Cerro Catedral, and Torres del Paine, among others, are considered a combination of arêtes and horns and nunataks (Fig. 4.5c). Small depositional glacial landform is mainly constituted by moraine deposits associated to the Little Ice Age (LIA, AD 1400–1750, Fig. 4.5c). Based on dendrochronological analysis of the trees colonizing the successive moraine ridges, the LIA extended between middle seventeenth and middle nineteenth centuries, indicating two neoglacial advances (Rabassa et al. 1984).

The fluvial action of this region is represented by braided rivers forming both from the thaw of glaciers and snow accumulation during winter. In the Argentinean side streams converge in main allochthonous rivers (e.g., Negro, Colorado, Chubut, and Santa Cruz) that cross the Extra-Andean Patagonia and flow into the South Atlantic Ocean. They have extensive fluvial valleys (disproportionate valleys) with successive terraces produced during the past glaciations. The mass wasting landforms in Southern Andes Cordillera (and in general in the entire Andes) are mostly produced by freeze-thaw activity (frost action) that causes physical weathering entailing the talus cone formation, the pipkrake process (frost heaving by ice needle growth) and gelifluction.

4.4 Mountain Sector of the Neuquén Embayment

The Mountain Sector of the Neuquén Embayment (Bracaccini 1970) includes the Cordillera del Viento and the Sierra de Chachil, two range systems with N-S orientation situated to the east near the Cordillera Principal, but in the Andean foreland (Fig. 4.2). The Cordillera del Viento includes a volcanic landscape whose summits are Cerro Butalón (2986 m a.s.l.) and Cerro La Corona (2991 m a.s.l.). The cordillera del Viento is flanked by the Tromen volcano to the south (Fig. 4.6a; 3978 m a.s.l.) and by the Domuyo volcano to the north (Fig. 4.6b; 4709 m a.s.l), and these are the

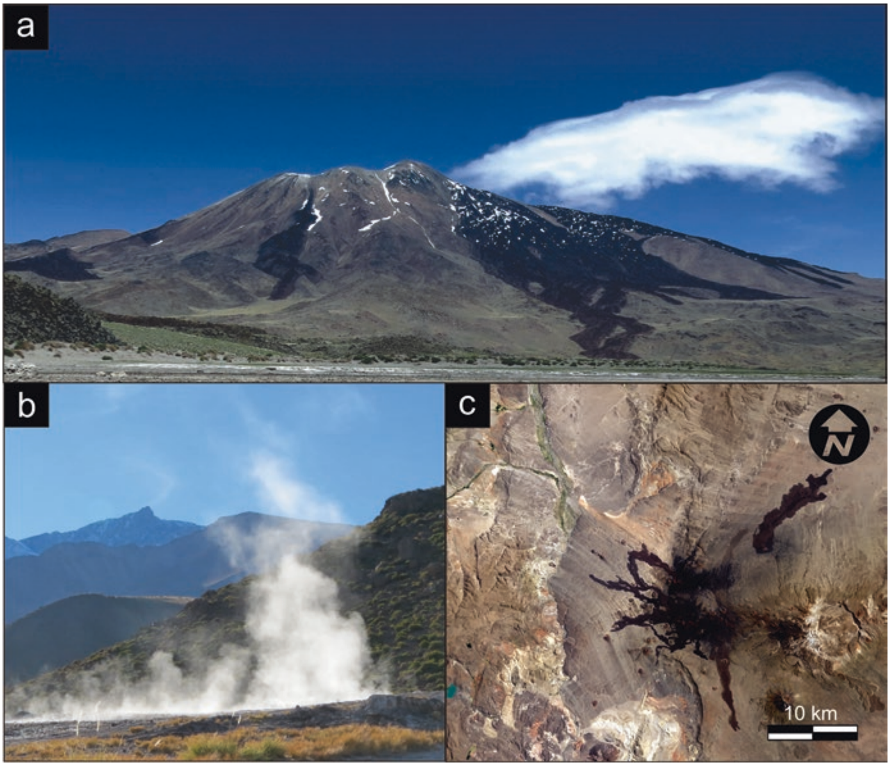

Fig. 4.6 Mountain Sector of the Neuquén Embayment, (**a**) Tromen volcano, (**b**) Domuyo volcano (foreground hydrothermal activity) (Tromen and Domuyo photographs courtesy of Dr. Leandro D'Elia), (**c**) Payún Matru volcanic field

largest mountain peaks of this region. The Sierra de Chachil (Cerro Chachil 2839 m a.s.l.) is situated 115 km west Neuquén city. The cordillera del Viento and Chachil Mountain ranges constitute blocks tectonically elevated that expose Paleozoic-Mesozoic rocks. In these outcrops, granitic, tonalithic, and granodioritic igneous bodies as well as rhyolitic dykes are recognized. Surrounding these outcrops, pyroclastic and sedimentary rocks from the continental origin of Mesozoic age also appear (Limarino et al. 1999). The volcanic landscape is constituted by calderas, volcanoes, and lava flows of Pleistocene-Holocene age, which represent basaltic distensive volcanism of retroarc type (chain of volcanoes formed above a subducting plate), as the Payún Matru volcanic field (Fig. 4.6c). Basic and acid to mesosilicic volcanic and pyroclastic rocks of Neogene age occur as outcrops forming discontinuous mountain ranges with an approximately north-south distribution. The Cerro Nevado (3773 m a.s.l.) is a volcanic massif situated to the east of Malargüe city, composed of volcanic and pyroclastic rocks of Neogene-Pleistocene age.

4.5 Northern Patagonian Tablelands

The Northern Patagonian Tablelands is a geological province defined in this chapter to refer to the developed plains of different origin located east and southeast of the Mountain Sector of the Neuquén Embayment (Fig. 4.2).

The main tableland landforms are composed of (1) isolated remnants of the Pleistocene basalt plains (plateau), (2) stabilized aeolian fields and active dune fields, and (3) Piedmont levels of Neogene age (bajadas) located to the south of Buenos Aires Province and to the north of Río Negro Province (Fig. 4.7a).

The Plio-Pleistocene basalt plain includes the Sierra de Auca Mahuida (2253 m a.s.l.), a volcanic complex that includes more than 100 minor vents that provided basaltic flows that overlie the pre-Pliocene to Quaternary sedimentary deposits (Kay et al. 2007).

Stabilized aeolian fields are composed of sandy mantles and dune fields of Late Pleistocene age; they extend across the southern most part of Buenos Aires, southern La Pampa, and northern Río Negro. In this geomorphological unit, linear, parabolic, barchanoid, and crescentic dunes are recognized (Fig. 4.7b, c) (Szelagowski et al. 2004; Zárate and Tripaldi 2012). These landforms are stabilized mainly with *Hyalis argentea* (olivillo). The active dune field is located in northeastern Río Negro Province on Golfo San Matías coast (east San Antonio Oeste); it has an eastward migration, mainly of transverse sand ridges.

Coalescing alluvial fans (bajadas) of Neogene-Quaternary period were developed in the eastern piedmont of the Mountain sector of the Neuquén Basin. These landscapes have eastern-southeastern distribution and their deposits are constituted of gravel and sand. Embedded into these old coalescing alluvial fans, fluvial terrace levels of the Colorado and Negro Rivers were developed.

On some intertidal areas, small coastal salt marshes occur. These landforms develop in the intertidal zone where a generally muddy substrate supports varied and normally dense stands of halophytic plants mainly *Spartina* genus. The representative salt marshes are located in the estuarine sector of the Negro River (El Cóndor beach), Caleta Los Loros, and San Antonio Oeste (Fig. 4.7d, e).

4.6 The North Patagonian Broken Foreland and Somún Curá Massif

The Patagonian Broken Foreland region defined in this work as part of the Patagonian broken foreland (Fig. 4.8a, sensu Bilmes et al. 2013), bounded to the north by the Río Limay and to the south by the southern end of the Sierra de San Bernardo (Figs. 4.2 and 4.8a). This region includes three geological provinces described by Ramos (1999): (a) the Precordillera Patagónica to the northwest, (b) the Bernárdides to the southeast, and (c) the western sector of the Meseta Patagónica Norte where there are outcrops of Mesozoic rocks from the Cañadón Asfalto Basin (Fig. 4.2).

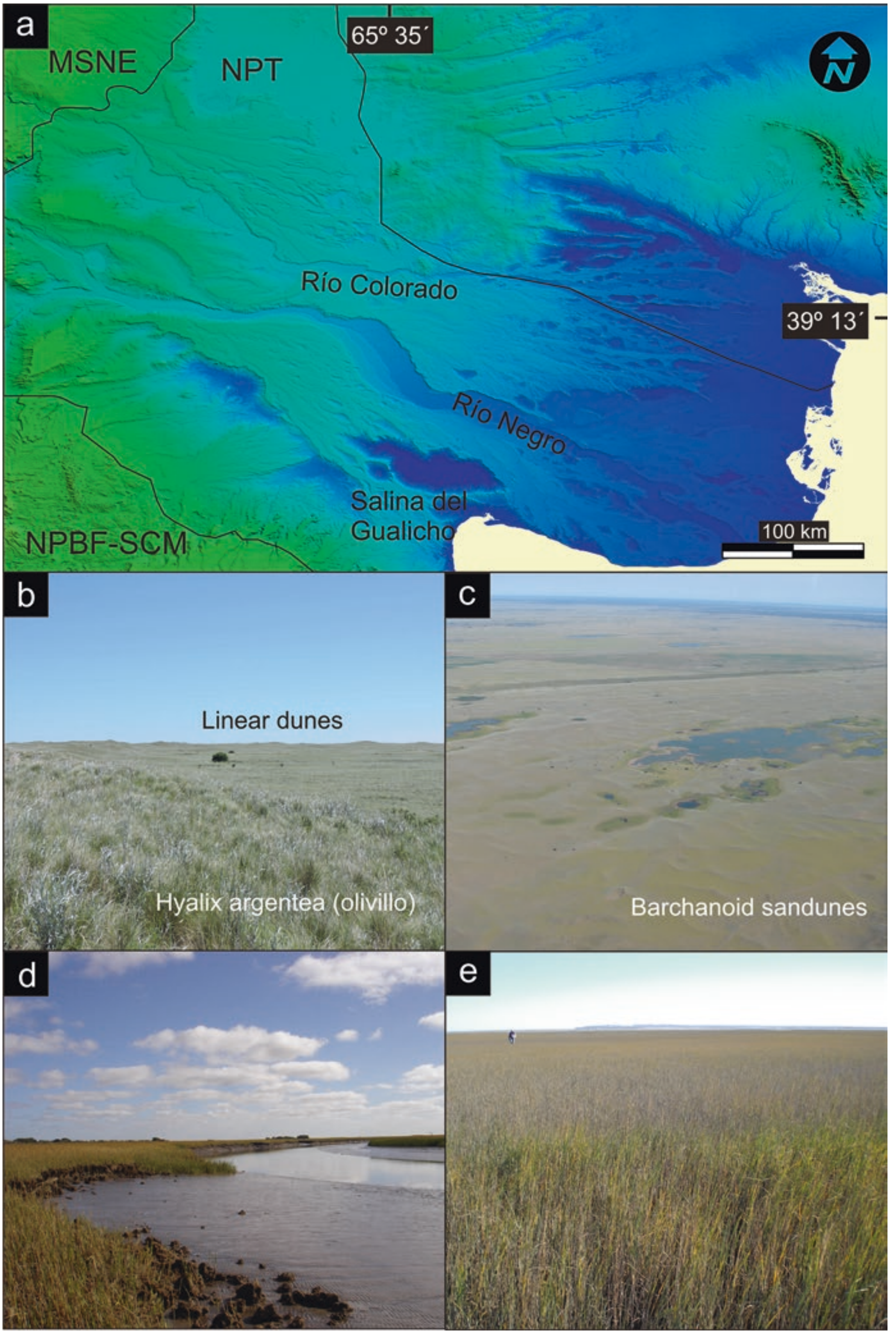

Fig. 4.7 (**a**) DEM showing the Northern Patagonian Tablelands region (NPT); MSNE Mountain Sector of the Neuquén Embayment, NPBF-SCM Patagonian Broken Foreland and Somún Curá Massif; (**b**) stabilized aeolian fields are composed of sandy mantles and dune field complex (linear, parabolic, crescentic dunes); (**c**) barchanoid sand dunes (**b** and **c** photographs courtesy of Dra. Adriana Mehl); (**d**) El Cóndor salt marsh (Negro River estuary, muddy intertidal); (**e**) Caleta Los Loros salt marsh (sandy intertidal) (salt marshes photographs courtesy of Dr. Alejandro Bortolus)

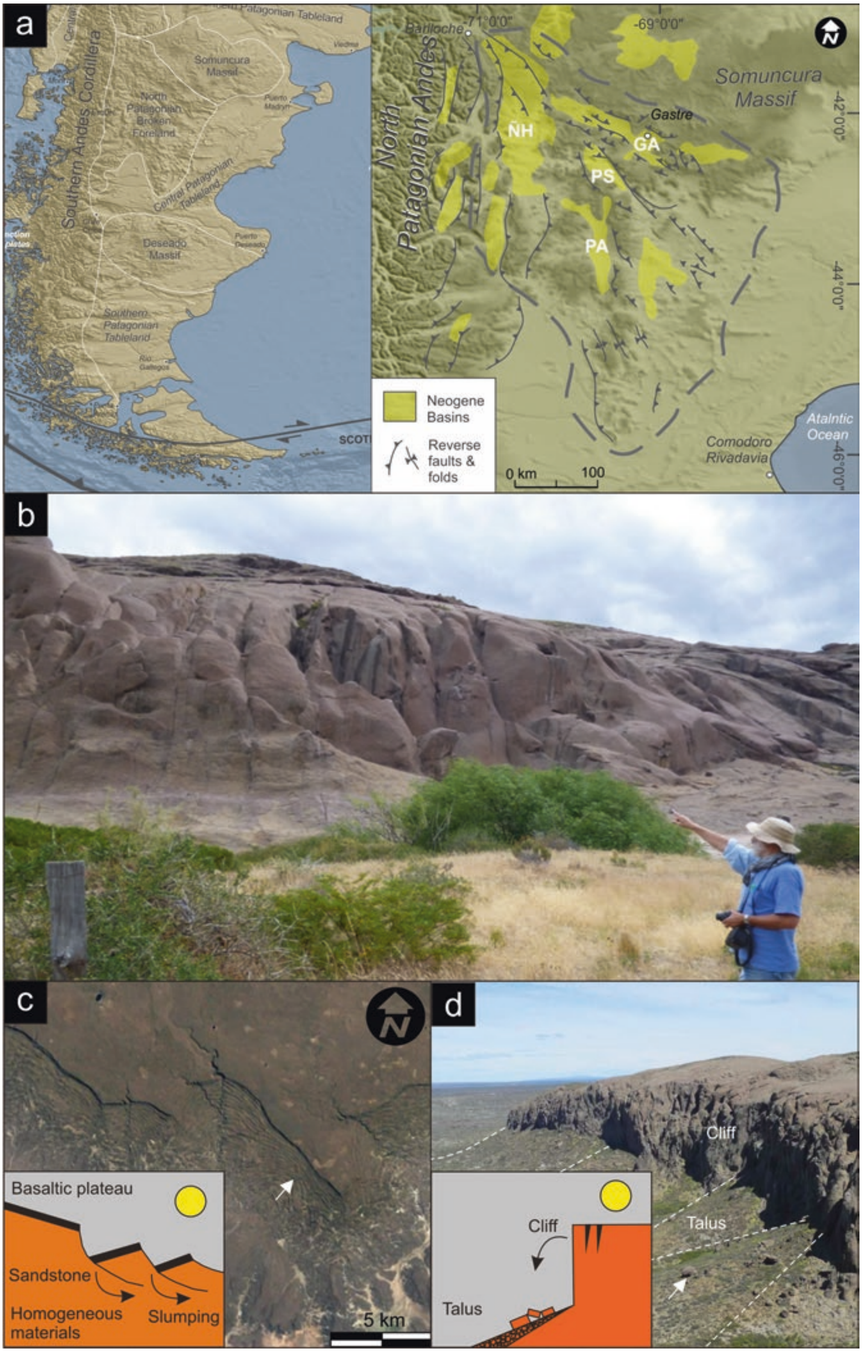

Fig. 4.8 (**a**) The Patagonian Broken foreland and Somún Curá Massif, (**b**) exhumed planation surfaces (Marifil Formation), (**c**) slumping in basaltic plateaus, (**d**) rockfall

This region is characterized by Neogene-Quaternary intermontane basins (e.g., Gastre Basin, Paso del Sapo Basin, Agnia Basin, Ñirihuau Basin) surrounded by fault block mountain ranges constituted by a Paleozoic-Triassic crystalline basement, uplifted Jurassic-Cretaceous sedimentary and volcanic deposits, and volcanic Paleogene rocks (Cazau et al. 1989; Bilmes 2013; Bucher et al. 2018; Fig. 4.8a). The Quaternary record of the intermontane basins includes fluvial-alluvial deposits, playa lakes, and lakes (*salinas*) and lava flows (Massaferro et al. 2006; Bilmes et al. 2017b).

The Somún Curá Massif received its denomination due to Precambrian features of their basement (Ramos 1999) and forms a complex landscape composed of exhumed planation surfaces and extended basaltic plateaus. Between these dominant features, other aggradational and erosional units developed as pediment association levels, fluvial terraces and alluvial fan levels (moderns and relicts), alluvial plains, wetlands (*mallines*), and endorheic basins. Exhumed planation surfaces correspond to Gondwana paleosurfaces and are the result of deep chemical weathering and/or pedimentation processes, occurred in very stable tectonic environments and mostly under hypertropical climates, extremely wet, or seasonally changing (Rabassa et al. 2010, 2014). In the Somún Curá Massif, the exhumed planation surfaces are easily recognized by their rounded hills and include Permian to Jurassic volcanic and plutonic rocks (Fig. 4.8b). The processes responsible for landscape modeling are due to a combination of spheroidal, chemical, and physical weathering. Physical weathering is reinforced by the displacive effect of the aeolian influx and subsequent pedogenesis (e.g., calcretization; Bouza et al. 2017b) between expansion joints.

One of the most important features of the Somún Curá Massif is the presence of basaltic plains constituting the actual positive relief, so constituting a dominant plateau landscape. This plateau landscape is composed of mafic lava flows and smaller volumes of silicic volcanic rocks associated with large shield volcanoes of late Oligocene to Early Miocene age (Ardolino and Franchini 1993; Kay et al. 2007). The exogenous geomorphic processes dominant in basaltic plateaus are mass wasting (gravitational), mainly by rotational movement or slumping and rockfall (Fig. 4.8c, d).

4.7 Central Patagonian Tablelands

The Central Patagonian Tablelands defined in this section comprises the plateaus of the central region of Chubut and north of Santa Cruz, between Somún Curá and Deseado Massifs, and to the east of the Patagonian Broken Foreland (Fig. 4.2). The landscape of this geological province is composed of erosional and aggradational geomorphic surfaces (surfaces defined in space and time terms) and by basaltic plateaus.

The erosional geomorphic surfaces are represented by badlands and pediment associations developed on sedimentary rocks. A pediment is defined by a gently and short slope transport surfaces of bedrock, covered by a thin alluvium, developed between an upland area where erosion dominates (i.e., the erosion scarps) and a lower plain where active aggradation dominates (i.e., *bajadas* or coalescent alluvial fans; Dohrenwend and Parsons 2009). In the Central Patagonian Tablelands, the erosional landscape is developed on continental sedimentary rocks, mainly of the Chubut Group (Jurassic-Lower Cretaceous) in the central Chubut Province (Fig. 4.9a, b), and on continental and marine sedimentary rocks of the Paleogene and Neogene period (e.g., Sarmiento, Gaiman, and Puerto Madryn formations) eastward. The pediment associations are highly dissected and present several levels caused by local changes in base level (Bouza et al. 2017a, b).

The aggradational geomorphic surfaces include coarse sediments that build alluvial/fluvial fans/*bajadas* that connect the pediment to either playa lakes in endorheic basins or gravel/sand beaches in the Atlantic coastal zone. The great endorheic basins are characterized by a typical centripetal drainage network (Fig. 4.9c, d). The main great endorheic basins in Patagonia are the Gran Bajo de San Julián (−105 m a.s.l.) in Santa Cruz Province, Bajo del Gualicho (−72 m a.s.l.), Bajo de la Tierra Colorada (60 m a.s.l.), Salina Grande (−43 m a.s.l.), Salina Chica (−19 m a.s.l.), Gran Salitral (0 m a.s.l.), and Bajo del Diablo (38 m a.s.l.) in Chubut Province. There are many controversies about the geomorphologic processes that originated these landforms. Whereas wind erosion was proposed to explain the formation of the endorheic basins, for example, in the Península Valdés region (Mouzo et al. 1978; González Díaz and Di Tommaso 2011), tectonics was also proposed (Roveretto 1921; Kostadinoff 1992; Isla 2013) and a combination of both processes was also suggested (Kostadinoff 1992; Haller et al. 2000). Although wind erosion could have been important, tectonic activity related to fault blocks probably triggered the formation of the great endorheic basins (Bouza et al. 2017b). This is supported by (1) the occurrence of closed basins formed on pebble gravel deposits that cannot be removed by deflation, (2) borders of the major depressions which are straight and in many cases match with subsurface faults (see Kostadinof 1992), and (3) post-Miocene faults which were observed in the region (Haller et al. 2000; Haller 2017).

The aggradational geomorphic surfaces are represented by old fluvial and marine terraces of Neogene-Quaternary period. The fluvial terrace relicts correspond mainly to the informal geological unit named Rodados Patagónicos (Plio-Pleistocene; Fidalgo and Riggi 1970). The genesis of this unit is related to old pluviofluvial and glaciofluvial plains widely distributed in the region, formed during the Neogene-Quaternary glaciations and deposited in an arid periglacial environment (Mercer 1976). On the Atlantic coast, these plains are composed of several terrace levels that descend in steps from southwest to northeast, with altitudes from 750 m a.s.l. (Pampa del Castillo) to 90 m a.s.l. around Puerto Madryn (Fig. 4.9d). The youngest plains generally present a braided type of paleo-drainage that is highlighted by a shrub vegetation pattern. In the Peninsula Valdés the Rodados Patagónicos extend widely at 50 m a.s.l, whereas only some relict surfaces reach 90 m a.s.l. (Bouza 2012).

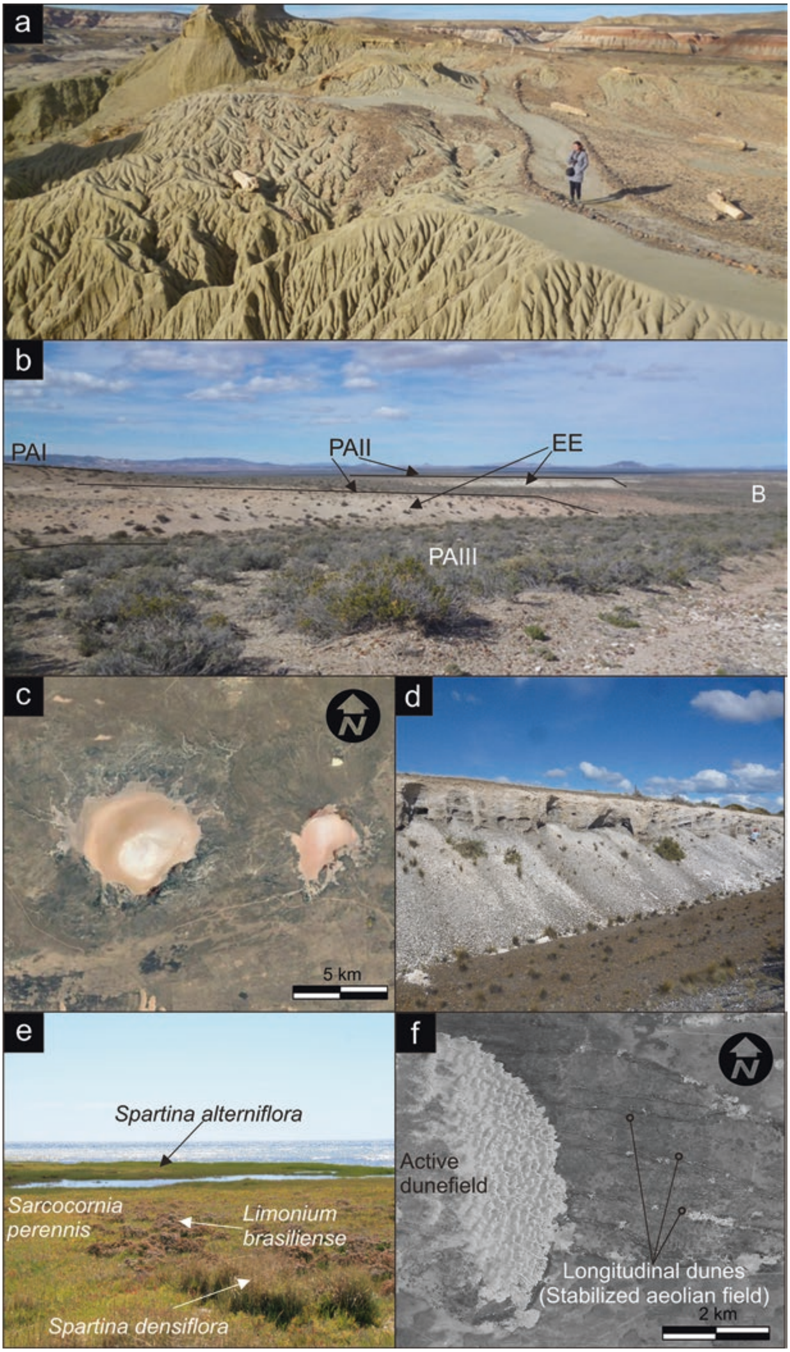

Fig. 4.9 Central Patagonian Tablelands; (**a**) Badlands, Sarmiento Petrified Forest; (**b**) pediment association levels (PA I-III); EE erosion scarp on sedimentary rocks (Chubut Group); bajada (B) (taken with modifications from Bouza et al. 2017b); (**c**) great endorheic basins in Península Valdés, centripetal drainage network; (**d**) detail of sedimentary structure of a Rodados Patagónicos terrace level; (**e**) *Sarcocornia* marsh, Fracasso beach, Golfo San José, Península Valdés; (**f**) stabilized aeolian fields and active dune field, Península Valdés

The current alluvial plains are present either linked to the allochthonous rivers (e.g., Chubut, Chico, and Deseado Rivers) or to ephemeral creeks, tributary streams, and bajadas of endorheic basins. Wetlands, locally named *mallines*, are located in restrained areas where the underground water discharge at the thalweg sectors of the channels.

Ancient marine terraces are distributed discontinuously along the Atlantic coast and were used to reconstruct changes in sea level that occurred during the Neogene-Quaternary through morpho-stratigraphic studies (Feruglio 1949–1950; Codignotto et al. 1992; Rostami et al. 2000; Pedoja et al. 2011). The malacological analysis of bivalves and gastropods housed in these deposits constituted the basis for the paleoclimatic reconstruction of the sea surface during the interglacial periods (Aguirre et al. 2008). Also, studies of paleosols developed on these terraces contributed to estimate the paleoenvironmental changes in continental environments (Schellmann and Radtke 2000; Bouza 2014).

The coastal landforms along the Atlantic shoreline in this sector are characterized by an alternation of headlands and bays, which due to the process of water wave diffraction erosion predominates on cliffs and wave-cut platforms and accretion on the beaches. The current accretional landforms are sandy and gravelly pocket beaches, formed between headlands of sedimentary rocks. Due to a combination of littoral drift and diffraction waves, accretional spits are formed (e.g., Caleta Valdés in Chubut). In sectors, the marine erosion is more prominent, reaching rectification of the coastline. Cliffs are developed on marine sedimentary rocks, mainly of Miocene age, when wave breakers impacted on the coast destabilizing the slope and promoting rockfall (mass wasting processes). This produces the cliff retreat and generates the wave-cut platform. On the other hand, when the Marifil Formation outcrops along shoreline, it is irregular due to resistance to marine erosion that offers these igneous rocks. The accretional landforms are sandy and gravelly pocket beaches, formed by wave diffraction between these outcrops of igneous rocks that emerged in the shoreline.

Spartina marshes are more common and larger in the northern part of Patagonia (latitudes lower than 42°S), while *Sarcocornia* marshes at latitudes higher than 42° S (Fig. 4.9e), and these two marsh physiognomies overlap between 42° S and 43° S (Bortolus et al. 2009).

The aeolian environment is noticeable mainly on the Atlantic coast landscape and in the southern sector of the Península Valdés, where two sub-geomorphology units are recognized: stabilized aeolian fields and active dune fields (Fig. 4.9f).

Stabilized aeolian fields have a well-developed vegetation cover of grasses (mainly *Sporobolus rigens*) and shrubs (principally *Hyalis argentea*). This unit stretches from the west to the east coast (i.e., from the Golfo Nuevo to the open Atlantic coast). In turn, the stabilized aeolian landforms are represented by a 0.4–2-m-thick sandy layer (Fig. 4.9f). In the aeolian field, the general orientation of the dunes is in agreement with the prevailing regional wind flow from the west-north-west. The sources of windblown sediment are the extensive sandy beaches located on the western coast of Golfo Nuevo, where a continued supply of loose, sand-sized sediment is available to be transported inland by the prevailing westerly winds. There is an eastward migration of the active dune fields to an average speed of 9.1 ± 2.7 m year^{-1} (annual rate 1969–2002; del Valle et al. 2008).

The basaltic plateaus (lava flows and volcanic necks) of Late Eocene to Pleistocene age extend east of the Patagonides and north of the Muster-Colihue Huapi lakes (Bruni et al. 2008).

4.8 Deseado Massif

The Deseado Massif has been considered as an ancient massif independent from the Somún Curá Massif already described (Fig. 4.2). It is a geological province located between the Deseado and the Chico Rivers in the Santa Cruz Province, characterized by its tectonic stability, for which it is considered a nesocraton, due to its stable and sub-positive relief during the Paleozoic (Ramos 1999).

The basement of the Deseado Massif is characterized by a sequence of metamorphic rocks of Upper Proterozoic-Lower Cambrian age. Granitoids and subvolcanic rocks of Silurian age intrude into these metamorphic rocks. Continental sequences of Permian and Triassic ages deposited on this basement were intruded by acid rocks of Upper Triassic-Lower Jurassic age.

These last intrusions correspond to a generalized extension linked to the opening of the Atlantic Ocean, followed by a clastic continental sequence, interdigitated with the rhyolitic volcanism of the Chon Aike Formation (Late to Middle Jurassic). These rhyolites and pyroclastic flows constitute an extensive plateau that in general constitutes, as the Somún Curá Massif, a wide exhumed planation surface.

The irregular coastal landforms along Atlantic shoreline in Deseado Massif have the same characteristics of coastal zone in Somún Curá Massif, with igneous rocks from Chon Aike Formation outcrop on the shoreline.

4.9 Southern Patagonian Tableland

The Southern Patagonian Tableland is located south of the Deseado Massif and east of the Southern Patagonian Andes (Fig. 4.2). The substratum of these plains is constituted by Mesozoic and Cenozoic deposits of the Austral-Magellan basin.

The northern sector of the plateau is formed by extensive alkaline basaltic casts of Miocene to late Pliocene (Camusú Aike Volcanic Field, tablelands on the north side of the Santa Cruz River valley, Meseta del Viento, Meseta de la Muerte, and Meseta Strobel); toward the south, the basalts form smaller plateaus and are replaced by large plateaus of Rodados Patagónicos (Miocene-Pleistocene age). These gravel terraces are dissected by wide valleys with glacial and fluvioglacial deposits.

At the central part of the Southern Patagonian Tableland is the Pali-Aike volcanic field (late Pliocene-Quaternary), where three postglacial volcanic cycles have been distinguished (Fig. 4.10). The oldest event originated *maars* while the last two episodes formed cones and lavas that cover most of the region (Skewes 1978). Based on archaeological and geomorphological evidence, it is presumed that the last volcanic event, which resulted in the formation of Cerro Diablo, occurred within the last 15 ka. The area covered by cones and lavas of Campo Pali-Aike exceeds 3000 km^2 across Chilean-Argentine border. The *maars*, originated by the first volcanic event, are formed by very violent volcanic explosions when the rising magma reacts violently with the water table (Fig. 4.10a). The intermediate volcanic episode gave rise to slag cones and lava flows that cover a large part of the Pali-Aike volcanic field and often appear covered by soils of aeolian origin (oldest lava flows). The most recent volcanic event originated the Cerro Diablo, which constitutes a pyroclastic cone. The lavas of the Cerro Diablo present few signs of erosion and soil development (Fig. 4.10b–d).

This geological province continues southward, beyond the Straits of Magellan, in the Extra-Andean region of Tierra del Fuego, with similar characteristics, although there are no basalt flows as in the Santa Cruz Province.

The dominant landform in the Extra-Andean region of Tierra del Fuego is composed of an erosion surface from marine sedimentary rocks of Paleogene to Neogene age (Fig. 4.10e). These surfaces were dissected and filled by morainic and fluvioglacial deposits, terraced fluvial deposits of Pleistocene epoch, and alluvial and colluvial deposits of Holocene epoch. A notable geomorphological feature in this region is the presence of numerous deflation hollows or pans (atmospheric dust sources), which become bodies of water or temporary lagoons of importance for migratory birds (Fig. 4.10f; Coronato et al. 2017).

The piedmont areas from the Southern Andes Cordillera were extensively glaciated, mainly by giant outlet glaciers coming from Patagonian Ice Sheets (Rabassa et al. 2011; Fig. 4.3). Andean lakes, U-shaped valleys, and marine channels (e.g., Estrecho de Magallanes and Canal de Beagle) evidence the advance of paleo-ice lobes. In addition to glacial moraines, other types of glacial drift deposits are named drumlins. These are located next to the Estancia Harberton (Harberton drumlin field) and were formed in the direction of the paleo-Beagle glacier flow. These landforms are elongate and streamlined hills composed largely of glacial deposits.

4.10 Islas Malvinas Plateau (Plateau de Las Islas Malvinas)

This region was described in the pioneering work of Darwin (1846), Thomson (1877), and Halle (1912). The Islas Malvinas are two islands, Isla Gran Malvina and Isla Soledad, located within the Argentine continental platform in the Malvinas Plateau, 500 km east of the Patagonian coast (Fig. 4.2). The geology of the area is dominated by outcrops of Paleozoic age intruded by Jurassic dykes that are partially

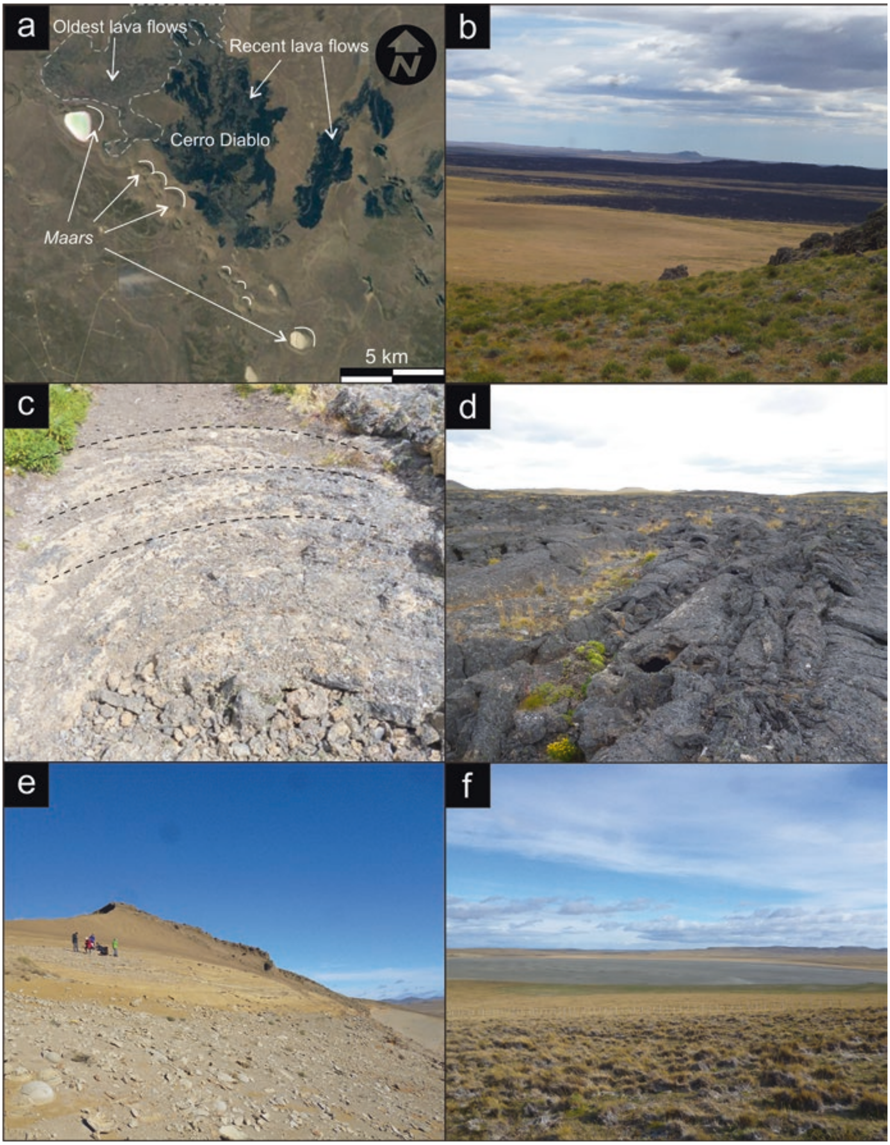

Fig. 4.10 Southern Patagonian Tableland, (**a**) Pali-Aike volcanic field, (**b**) lavas of the Cerro Diablo, (**c**) corded lavas or pahoehoe type, (**d**) structures of lava tunnels, (**e**) erosional landscape on marine sedimentary rocks of Paleogene and Neogene period in Tierra del Fuego, (**f**) deflation hollows or pans

or completely covered by Quaternary deposits. This region is part of a Gondwana paleosurface, conforming a landscape dominated by rounded hills (Fig. 4.11a–c). The Quaternary deposits include the amazing deposits of the classic stone runs (Fig. 4.10a, d), marine clays and sands, windblown sand, alluvium, and an extensive

Fig. 4.11 Malvinas Plateau (Plateau de Las Islas Malvinas); (**a**–**c**) landscape characterized by rounded hills; (**d**) stone runs (Malvinas photographs courtesy of Dr. Fernando Coronato)

cover of blanket peat (Stone 1999). In the highest ground, a few small cirque glaciers exist (Clapperton and Sugden 1976), but for the most part the conditions were of deep-frozen tundra indicating that the islands never experienced any substantial ice cover. The "stone runs" (Fig. 4.11d) are peculiar stone rivers developed on such a large scale that their extensions can only really be appreciated from the air (Stone 1999). Their origin is controversial, while some agree that their formation is related to periglacial activity (Bellosi and Jalfin 1984; Rosenbaum 1996; Hansom et al. 2008), others consider a complex polygenetic origin associated with subtropical weathering (André et al. 2008).

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Chapter 5
Vegetation of Patagonia

Alejandro Jorge Bisigato and Mónica Beatriz Bertiller

Abstract In this chapter, we describe the major phytogeographic provinces of Patagonia. Emphasis is placed on physiognomic vegetation formations, internal heterogeneity, and degree of anthropic disturbance. Main vegetation formations within provinces include temperate forests, steppes, moorlands, and shrublands. Internal plant heterogeneity is high in all provinces and is associated with climate, soils, altitude, and natural (e.g., volcanism) or anthropogenic disturbances. The most important anthropogenic disturbance varies among provinces in relation to vegetation formations. Domestic grazing is a widespread disturbance agent in steppes and shrublands, while oil and natural gas extraction may also cause disturbances affecting local plant communities in some areas. In contrast, clearing for agriculture and afforestation are common in temperate forests. Invasion of exotic plants and animals are also a threat for the conservation of pristine vegetation. Disturbances, together with the ongoing climate change, can strongly influence vegetation structure and functioning that in turn could affect populations of wild animals, particularly lizards.

Keywords Patagonia · Vegetation heterogeneity · Climate · Disturbance · Grazing · Deforestation/afforestation

5.1 Introduction

Patagonian vegetation encompasses a wide range of physiognomic vegetation formations from forests to arid steppes and moorlands. In general, most studies of Patagonian vegetation were restricted either to Chilean (e.g., Quintanilla Pérez 1985, 1989; Gajardo 1994; Luebert and Pliscoff 2006) or Argentinean Patagonia (e.g., Soriano 1956, 1983; León et al. 1998). Syntheses attempting to gather descriptions

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A. J. Bisigato (✉) · M. B. Bertiller
Instituto Patagónico para el Estudio de los Ecosistemas Continentales – Consejo Nacional de Investigaciones Científicas y Técnicas (IPEEC-CONICET),
Puerto Madryn, Chubut, Argentina
e-mail: bisigato@cenpat-conicet.gob.ar; monika@cenpat-conicet.gob.ar

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of vegetation made in both countries are infrequent (e.g., Heusser 2003; Gut 2008) mainly due to different approaches, perspectives, and methods used to delimit different "vegetation units." As in the rest of this book, we refer to Patagonia as the area delimited by the Tinguiririca, Atuel, Salado, Chadileuvu, and Colorado rivers. Following Morrone (2001a) and Morrone (2004, 2006), most of this area belongs to the Andean Region. Only the northern extreme in the Argentinean Patagonia occupies part of the South American transition zone (Urtubey et al. 2010), to which Morrone reassigned some provinces previously ascribed to the Neotropical region (Morrone 2004, 2006). Overall, we followed the classification of Morrone (2001a), who in his book *Biogeografía de América Latina y el Caribe* analyzed Patagonian vegetation without restrictions due to country limits, along with subsequent descriptions modifying some boundaries among provinces in Morrone (2014, 2015). The names of some provinces (but not their limits) were modified according to more recent works (e.g., Morrone and Ezcurra 2016).

Patagonian vegetation mirrors the marked climatic differences across the region imposed by the elevation of the Andes Mountains, disrupting the large-scale circulation of air masses. In fact, the Andes have a critical influence in determining the climate of Patagonia by imposing a barrier for humid air masses from the Pacific Ocean. As a consequence, most of water is discharged at the west slope of the Andes (on the Chilean side) and dry and hot air descends at the east side of the Andes over the Argentinean Patagonia (Paruelo et al. 1998; Labraga and Villalba 2009). Accordingly, forests and moorlands occupy most of the Chilean Patagonia, whereas the largest area of the Argentinean Patagonia is part of the South American Arid Diagonal covered by steppes, semideserts, and shrublands. In this context, Patagonian forests have evolved since the Pliocene in isolation from other South American forests being more closely related to Australian and New Zealand forests (Villagrán and Hinojosa 1997; Villagrán and Armesto 2005). Latitude, as a surrogate of temperature, also affects plant distribution along this extended region. For example, the tree line is at 2150 m at 33° S but descends to 350 m at 55° S (Heusser 2003). Vegetation heterogeneity due to differences in soil attributes is also present at finer scales than those imposed by climate (e.g., Rueter and Bertolami 2010; Palacio et al. 2014; Casalini and Bisigato 2017). Across Patagonia, azonal plant communities occupy small areas with particular soil attributes conditioning higher or lower water availability than at zonal communities. For example, azonal wet meadows, locally known as *mallines*, with more mesic vegetation than the surrounding steppes may be found in arid Patagonia (Soriano 1983; Buono et al. 2010; Gaitán et al. 2011). Similarly, a strong local soil-vegetation relationship may be found at the forest humid sites, where zonal forest vegetation may include patches of azonal grasslands and *Sphagnum* bogs (Holdgate 1961). Despite this, only regional zonal vegetation formations will be considered in this chapter.

In the next sections we present a general description of vegetation of the Patagonian phytogeographic provinces including dominant physiognomies, the most common species, and a mention of their internal heterogeneity. A detailed description (and mapping) of vegetation units inside provinces (e.g., districts) is out of the scope of this chapter, since previous studies provided excellent detailed descriptions (e.g., Soriano 1956; Gajardo 1994; León et al. 1998; Luebert and Pliscoff 2006). Furthermore, there are many studies describing and mapping plant assemblages in different areas of Patagonia (e.g., Bertiller et al. 1981, 2017; Quintanilla Pérez 1985, 1989; Beeskow et al. 1987; Rueter and Bertolami 2010; Bisigato et al. 2016). Due to its extension and great variability, we exceptionally briefly describe subprovinces within the Patagonian Province. Plant nomenclature follows *Flora Argentina* (http://www.floraargentina.edu.ar/) for Argentinean species and *Catálogo de las Plantas Vasculares de Chile* (Rodríguez et al. 2018) for the Chilean flora. Authorities for species names are detailed in Appendix.

5.2 Phytogeographic Provinces

5.2.1 South American Transition Zone

5.2.1.1 Monte Province

The Monte Province occupies 526,000 km^2 in west Argentina (Bisigato et al. 2009) but only 280,300 km^2 cover the northeastern Argentinean Patagonia. This portion of the territory is located east of the isotherm of 13° C, reaching 44° S (Morrone 2001a; Rundel et al. 2007; Abraham et al. 2009; Oyarzábal et al. 2018) (Fig. 5.1). Precipitation ranges from 116 to 200 mm (Labraga and Villalba 2009, Coronato [Chap. 2]). Vegetation is characterized by shrubby plant communities dominated by species of the genus *Larrea* (*L. divaricata*, *L. nitida*, *L. ameghinoi*, and *L. cuneifolia*; Fig. 5.2). Other common shrubs are *Prosopis flexuosa*, *P. alpataco*, *Prosopidastrum striatum*, *Monttea aphylla*, *Bougainvillea spinosa*, *Condalia microphylla*, and several species of the genus *Lycium*, *Chuquiraga*, and *Gutierrezia* (León et al. 1998; Oyarzábal et al. 2018). Grasses of the genus *Poa*, *Pappostipa*, and *Nassella* are common, especially at the southern extreme of this province. In general, plant cover is low but it increases near the Atlantic Ocean due to greater precipitation (León et al. 1998). In this area, small groups of *Geoffroea decorticans* individuals are common. Overgrazing is a widespread disturbance (Bisigato and Bertiller 1997; Tadey 2006; Villagra et al. 2009), but impacts by vegetation removal for hydrocarbon extraction are particularly important in the north (Neuquén Province) (Radovani et al. 2014). Wildfires are also common (Hardtke et al. 2011) deeply affecting vegetation structure and function (Rostagno et al. 2006; Villagra et al. 2009).

5.2.1.2 Cuyan High Andean Province

The Cuyan High Andean Province, originally named Prepuna Province (Morrone 2001a), extends mainly in western Argentina, reaching neighboring areas in central Chile, north of 38° S (Morrone and Ezcurra 2016) (Fig. 5.1). It includes several of the highest mountains of South America. Climate is windy and very cold (Arroyo

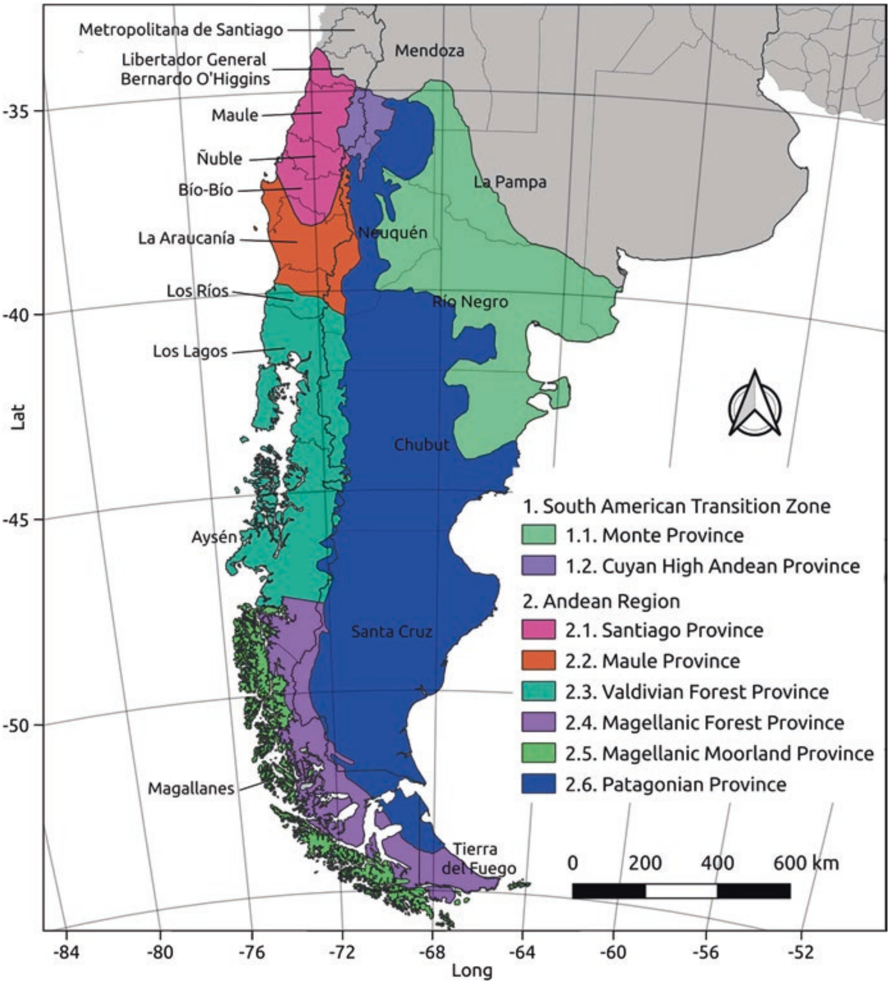

Fig. 5.1 Vegetation map of Patagonia. Redrawn from Romano (2017) showing the phytogeographical provinces and administrative divisions (regions in Chile and provinces in Argentina). We modified the northeastern limit of the Monte Province following Oyarzábal et al. (2018) and the western limit of the Cuyan High Andean Province following Luebert and Pliscoff (2006)

and Cavieres 2013). Only the southern extreme of this province is included in Patagonia, covering 19,900 km^2. Dominant species are a mixture of perennial herbs, low rounded shrubs, and cushion plants (Fig. 5.3): *Senecio algens*, *Oxalis compacta*, *Oxalis adenophylla*, *Pozoa coriacea*, *Laretia acaulis*, *Berberis empetrifolia*, *Chuquiraga oppositifolia,* and *Discaria articulata* (Luebert and Pliscoff 2006; Arroyo and Cavieres 2013; Oyarzábal et al. 2018).

Fig. 5.2 Monte Province. Dominant *Larrea divaricata* shrublands in the southern portion in Chubut, Argentina (Photo: A. Bisigato)

Fig. 5.3 Cuyan High Andean Province near Laguna del Maule, Chile (Photo: L. Avila)

5.2.2 Andean Region

5.2.2.1 Santiago Province

The Santiago Province is located north of 38° S and is the most arid province among the Chilean Patagonian provinces (Fig. 5.1). This is partially due to low precipitation induced by the coastal cordillera, but mostly to high temperatures and a summer dry season (Heusser 2003; Armesto et al. 2007). Only the southern tip of this province (62,900 km^2) is included in the Patagonian region, as defined in this book. Scrublands are the dominant physiognomy, although small Mediterranean woodlands can also be found (Morrone 2001a). Dominant species are *Vachellia caven*, *Peumus boldus*, *Fabiana imbricata*, *Lithraea caustica*, and *Quillaja saponaria* (Gajardo 1994; Heusser 2003; Luebert and Pliscoff 2006). Major threats to conservation are deforestation, wildfires, overgrazing, firewood collection, afforestation with exotic tree species, and invasion of exotic species (Morrone 2001a; Lara et al. 2012).

5.2.2.2 Maule Province

The Maule Province occupies 59,000 km^2 in Chile and Argentina, south of the province of Santiago (38° to 40° S, Fig. 5.1) (Morrone 2000; Gut 2008). Climate is humid and temperate without a dry season. Pristine vegetation is mostly represented by a deciduous forest, but it was almost completely converted to agricultural land (Gajardo 1994; Heusser 2003; Lara et al. 2012). In the few relicts of native vegetation, the dominant species is *Nothofagus obliqua*, but other cogeneric species are also common (*N. dombeyi*, and *N. alpina*). Different communities, co-dominated by *Austrocedrus chilensis*, *Laurelia sempervirens*, *Podocarpus saligna*, *Dasyphyllum diacanthoides*, *Cryptocarya alba*, and/or *Persea lingue* are distinguishable (Gajardo 1994; Heusser 2003; Luebert and Pliscoff 2006). On the coastal cordillera, pristine vegetation is co-dominated by *N. obliqua* and *Gomortega keule*, but it was almost completely replaced by *Pinus radiata* plantations. Primeval vegetation on the central valley was dominated by *N. obliqua*, accompanied by *N. dombeyi* at the north and by *L. sempervirens* at the south. Small forests of *Araucaria araucana* and *Nothofagus pumilio* can be found at altitudes higher than 1000 m (Fig. 5.4). Deforestation and afforestation with exotic tree species are the most important risks for vegetation conservation (Morrone 2001a; Lara et al. 2012; Franzese et al. 2017).

5.2.2.3 Valdivian Forest Province

The Valdivian Forest Province occupies 166,000 km^2 in Chile and Argentina, south of the Maule Province reaching 47° S (Morrone 2000, Fig. 5.1). Climate is cold, wet, and cloudy. In contrast to Maule Province, evergreen forest is the prevailing

Fig. 5.4 Maule Province. *Araucaria araucana* forest in Neuquén, Argentina (Photo: M. Bertiller)

physiognomy (Fig. 5.5). Deciduous forests are restricted to high altitudes on the coastal cordillera and the Andes. Tree canopies commonly reach 40 m in height. Lianas (e.g., *Hydrangea serratifolia*, *Griselinia ruscifolia*, etc.), epiphytic ferns (*Hymenophyllum caudiculatum* and *Polypodium feuillei*), and bamboo (*Chusquea quila*) are common (Heusser 2003). Near the coast, plant communities are dominated by *Aextoxicon punctatum* and *Eucryphia cordifolia.* Inland, dominant species are *Nothofagus dombeyi*, *Laureliopsis philippiana*, *Luma apiculata*, *Podocarpus nubigena*, *Fitzroya cupressoides*, *Saxegothaea conspicua*, *Weinmannia trichosperma*, and *Laurelia sempervirens* (Gajardo 1994; Heusser 2003; Luebert and Pliscoff 2006). *Nothofagus nitida* and *Podocarpus nubigena* dominate in the north of the island of Chiloé, while *Pilgerodendron uviferum* and *Tepualia stipularis* do it in the south. Vegetation of this province is very heterogeneous. It is partially due to its large latitudinal range, but also to altitudinal gradients and the presence of natural (volcanism) and anthropic disturbances (agriculture, afforestation, and fire). Some authors split this extensive province in two (e.g., Heusser 2003), reserving the name of Valdivian forest for the most diverse and dense communities found in the north.

5.2.2.4 Magellanic Forest Province

The Magellanic Forest Province goes from 47° S to Cape Horn, covering 107,000 km^2 (Morrone 2000; Fig. 5.1). It is located inland from the Magellanic Moorland Province. It is discontinued by the presence of fjord-like channels, glaciers, and ice fields and intermingled with moorlands. Most of this province lies in Chile, but it reaches Argentina in western Santa Cruz and Tierra del Fuego.

Fig. 5.5 Valdivian Forest Province. Evergreen forest in Termas del Amarillo Provincial Park, Chile (Photo: M. Bertiller)

Nothofagus betuloides is especially abundant in this province (Fig. 5.6). Other common species are *Maytenus disticha*, *Drimys winteri*, *N. pumilio*, and *N. antarctica*. The last species partially replaces *N. pumilio* to the east, where precipitation is low (Gajardo 1994; Heusser 2003; Luebert and Pliscoff 2006). In the periglacial areas a community co-dominated by *N. antarctica* and *Gunnera magellanica* is found (Gajardo 1994). Exotic animals (e.g., American beaver (*Castor canadensis*) and European rabbits (*Oryctolagus cuniculus*)) have deeply affected vegetation of this province, mainly in Tierra del Fuego (Jaksic 1998; Bortolus and Schwindt 2006; Baldini et al. 2008).

5.2.2.5 Magellanic Moorland Province

The Magellanic Moorland Province occupies 55,300 km^2 in southern Chile, although marginally reaches Argentina in Tierra del Fuego, between the coast and the Magellanic Forest Province (Morrone 2000; Fig. 5.1). Climate is humid (annual precipitation generally reaches 4000 mm), windy, and cold (Arroyo et al. 2005). As the province's name indicates, dominant physiognomy is the moorland. More or less

Fig. 5.6 Magellanic Forest Province. Nothofagus forest in Torres del Paine National Park, Chile (Photo: M. Bertiller)

extended areas of exposed rocks are common. Most frequent species are *Empetrum rubrum*, *Oreobolus obtusangulus*, *Astelia pumila*, *Donatia fascicularis*, *N. betuloides*, *N. pumilio*, and *Sphagnum magellanicum* (Gajardo 1994; Arroyo et al. 2005). Tree species are restricted to well-drained areas sheltered from cold winds (Heusser 2003; Arroyo et al. 2005). As a consequence of its inaccessibility, disturbances are rare and mostly restricted to areas with tree cover (Arroyo et al. 2005).

5.2.2.6 Patagonian Province

The Patagonian Province occupies 549,300 km^2 most of them at southwestern Argentina, from Mendoza to Tierra del Fuego (Morrone 2001b) and only a small area in southern Chile. Plant physiognomy varies greatly across this extensive province, from semideserts and shrub steppes at central Patagonia to grass steppes at southern and western Patagonia (Paruelo et al. 2007). Accordingly, five main subprovinces can be defined (Payunia, Subandean, Western Patagonian, Central, and Magellanic; León et al. 1998; Morrone 2015). The Payunia Subprovince covers southern Mendoza and northern Neuquén associated with volcanic hills with sandy and basaltic soils. Vegetation are shrub steppes dominated by *Azorella prolifera* at the highest sites and by *Stillingia patagonica*, *Anarthrophyllum rigidum*, *Ephedra ochreata*, and *Colliguaja integerrima* at mid-altitudes (León et al. 1998). West from the Valdivian Forest and the Magellanic Forest Provinces, the Subandean Patagonian Subprovince is represented by a grass steppe dominated by the perennial grass *Festuca pallescens* among other perennial grasses (*Bromus setifolius*, *F. pyrogea*,

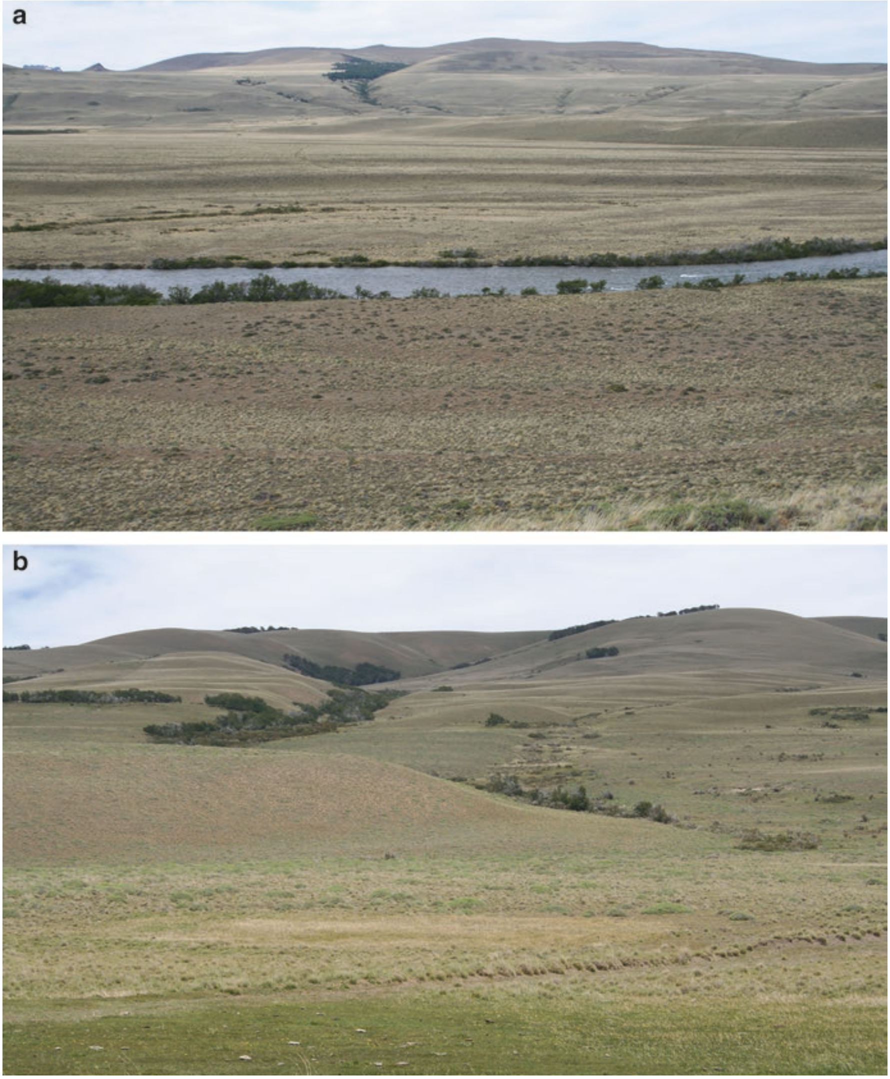

Fig. 5.7 Patagonian Province. Subandean Subprovince. *Festuca pallescens* steppes in alluvial terraces of Senguerr river in southwestern Chubut (**a**) and covering morainic hills in southwestern Chubut (**b**) (Photo: M. Bertiller)

Hordeum comosum, *Koeleria vurilochensis*, *Poa ligularis*, and *Rytidosperma virescens*) with sparse shrubs or patches of *Azorella prolifera* (Bertiller et al. 2006; Fig. 5.7). The Western Patagonian Subprovince consisting of grass-shrub steppes with a patchy structure occupies a narrow strip at the west of the area limiting with the Subandean Patagonian Subprovince. Plant patches include perennial grass species (*Pappostipa speciosa*, *P. humilis*, *Poa ligularis*, *Hordeum comosum*, and

Fig. 5.8 Patagonia Province. Western Subprovince. Shrub-grass steppes in Río Mayo, Chubut, Argentina (Photo: M. Bertiller)

Bromus setifolius) and shrub species dominated by *Azorella prolifera*, *Senecio filaginoides*, and *Adesmia volckmannii* (Soriano 1956; Golluscio et al. 1982) (Fig. 5.8). Shrub steppes and semideserts are the dominant physiognomy occupying the Central Subprovince located at the east of the Western Subprovince. Shrub steppes are mainly dominated by *Chuquiraga avellanedae* at the north with the accompanying species *Lycium ameghinoi*, *L. chilense*, *Mulguraea ligustrina*, and *Prosopis denudans* (Fig. 5.9a). At the south of this subprovince *Mulguraea tridens* is the dominant species with other less abundant species in the herbaceous layer (*Pappostipa ibarii*, *Jarava neaei*, *Pappostipa speciosa*, and *Festuca pyrogea*) (León et al. 1998). Semideserts are mainly dominated by the dwarf shrub *Nassauvia glomerulosa* along with the small shrubs *Chuquiraga aurea*, *C. morenonis*, *Petunia patagonica*, and *Azorella monantha* and the perennial grass *Poa spiciformis* (Fig. 5.9b). The Magellanic Subprovince occupies the southern portion of the Argentinian Patagonian Province and vegetation is represented by grass steppes dominated by *Festuca gracillima* and other perennial grasses and sedges (León et al. 1998; Peri et al. 2013). For more than a century, overgrazing has affected the structure and functioning of these Patagonian ecosystems (Soriano and Movia 1986; Ares et al. 1990; Bertiller et al. 1995; Oliva et al. 2016). Disturbance due to gas and oil extraction is locally severe in some areas (Bortolus and Schwindt 2006; Rueter and Bertolami 2010). Exotic plant invasions are common (Speziale and Ezcurra 2011; Speziale et al. 2013; Bravo-Monasterio et al. 2016; Franzese et al. 2017) and very serious in some areas as Tierra del Fuego (Cipriotti et al. 2010). The European hare (*Lepus europaeus*) has invaded most of this province (Jaksic 1998) and wild rabbits (*Oryctolagus cuniculus*) are invading part of this province in Tierra del Fuego and Neuquén (Bonino and Soriguer 2009).

Fig. 5.9 Patagonia Province. Central Subprovince. *Chuquiraga avellanedae* steppe in Los Altares, Central Chubut (**a**). Semidesert dwarf steppe of *Nassauvia glomerulosa* in alluvial terraces of the Senguerr river in south-central Chubut (**b**) (Photos: M. Bertiller)

5.3 Final Words

Patagonia encompasses a vast territory with high climatic and landscape heterogeneity modulating a high diversity of plant formations from forests to deserts. These plant formations are characterized by a high internal plant heterogeneity providing a high diversity of niches for lizard species (e.g., Llancapán 2005). A common feature of Patagonian plant formations is that anthropic disturbance is widely spread across the territory. This along with predicted global warming and climate change constitutes an alert in relation to changes in these formations affecting not only the structure but also the functioning of vegetation with impacts on main ecosystem processes and on the conservation and sustainability of animal populations. In fact, direct and indirect (i.e., vegetation mediated) effects of disturbances on lizard communities are almost completely unknown in Patagonia (but see Bonenti 2005).

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Appendix

Adesmia volckmanni Phil.
Aextoxicon punctatum Ruiz & Pav.
*Anarthrophyllum rigidum (*Gillies ex Hook. & Arn.) Hieron.
Araucaria araucana (Molina) K. Koch
Astelia pumila (G. Forst.) Gaudich.
Austrocedrus chilensis (D.Don) Pic.Serm. & Bizzarri
Azorella monantha Clos.
Azorella prolifera (Cav.) G.M. Plunkett & A.N. Nicolas
Berberis empetrifolia Lam.
Bougainvillea spinosa (Cav.) Heimerl
Bromus setifolius J. Presl.
Chuquiraga aurea Skottsb.
Chuquiraga avellanedae Lorentz
Chuquiraga morenonis (Kuntze) C.Ezcurra
Chuquiraga oppositifolia D. Don
Chusquea quila Kunth
Colliguaja integerrima Gill. & Hook.
Condalia microphylla Cav.
Cryptocarya alba (Molina) Looser
Dasyphyllum diacanthoides (Less.) Cabrera
Discaria articulata (Phil.) Miers
Donatia fascicularis J.R. et G. Forst.
Drimys winteri J.R.Forst. & G.Forst.
Empetrum rubrum Vahl ex Willd.
Ephedra ochreata Miers.
Eucryphia cordifolia Cav.
Fabiana imbricata Ruiz & Pav.
Festuca gracillima Hook.f.

Festuca pallescens (St. Ives) Parodi
Festuca pyrogea Speg.
Fitzroya cupressoides (Molina) I.M.Johnst.
Geoffroea decorticans (Gill. ex Hook. & Arn.) Burkart
Gomortega keule (Molina) Baill
Griselinia ruscifolia (Clos.) Taub.
Gunnera magellanica Lam.
Hordeum comosum J. Presl.
Hydrangea serratifolia (Hook. & Arn.) F. Phil.
Hymenophyllum caudiculatum Mart.
Jarava neaei (Nees ex Steud.) Peñail.
Koeleria vurilochensis C.E. Calderón ex Nicora
Laretia acaulis (Phil.) Reiche
Larrea ameghinoi Speg.
Larrea cuneifolia Cav.
Larrea divaricata Cav.
Larrea nitida Cav.
Laurelia sempervirens (Ruiz & Pav.) Tul
Laureliopsis philippiana (Looser) R.Schodde
Lithraea caustica (Molina) Hook. et Arn.
Luma apiculata (DC.) Burret
Lycium ameghinoi Speg.
Lycium chilense Bertero
Maytenus disticha (Hook.f.) Urb.
Monttea aphylla (Miers) Benth. & Hook.
Mulguraea ligustrina (Lag.) O'Leary & P.Peralta
Mulguraea tridens O'Leary & P.Peralta
Nassauvia glomerulosa (Lag. ex Lindl.) D. Don
Nothofagus alpina (Poepp. & Endl.) Oerst.
Nothofagus antarctica (G.Forst.) Oerst.
Nothofagus betuloides (Mirb.) Oerst.
Nothofagus dombeyi (Mirb.) Oerst.
Nothofagus nitida (Phil.) Krasser
Nothofagus obliqua (Mirb.) Oerst.
Nothofagus pumilio (Poepp. & Endl.) Krasser
Oreobolus obtusangulus Gaudich.
Oxalis adenophylla Gillies ex Hook. & Arn.
Oxalis compacta Gillies ex Hook. & Arn.
Papostipa humilis (Cav.) Romasch
Pappostipa ibarii (Phil.)Romasch.
Pappostipa speciosa (Trin. & Rupr.) Romasch
Peumus boldus Molina
Persea lingue Miers ex Bertero Nees
Petunia patagonica Millán
Pilgerodendron uviferum (D. Don) Florin

Pinus radiata D. Don
Poa ligularis Nees. ex. Steud.
Poa spiciformis (Steud.) Hauman & Parodi
Podocarpus nubigena Lindl.
Podocarpus saligna D.Don.
Polypodium feuillei Bertero
Pozoa coriacea Lag.
Prosopidastrum striatum (Benth.)R.A. Palacios&Hoc.
Prosopis alpataco Phil.
Prosopis denudans Benth.
Prosopis flexuosa DC.
Quillaja saponaria Molina
Rytidosperma virescens (E. Devs.) Nicora
Saxegothaea conspicua Lindl.
Senecio algens Wedd.
Senecio filaginoides DC.
Sphagnum magellanicum Brid.
Stillingia patagonica (Speg.) Pax & K. Hoffm.
Tepualia stipularis (Hook. & Arn.) Griseb.
Vachellia caven (Molina) Seigler & Ebinger
Weinmannia trichosperma Cav.

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Part III
Diversity and Current Knowledge of Patagonian Lizards

Chapter 6
The Patagonian Fossil Lizards

Adriana María Albino

Abstract The squamates constitute a significant part of the present-day South American herpetofauna, and their fossils provide crucial evidence for understanding the origin and evolution of the main clades. The fossil record of squamates in Patagonia is still scarce but it represents one of the most prolific of all of South America. An updated systematic review of the available information of Patagonian fossil lizards is summarized in this chapter. The oldest lizards of Patagonia are found as far back as the Upper Cretaceous and include materials referred to two of the most diverse extant clades: Iguania and Scincomorpha. Palaeocene and Eocene interestingly do not provide any lizard specimens from this time frame, but the record reappears in the Late Oligocene with iguanians. A significant increase in materials is revealed later in the Neogene. Early Miocene lizards include the first appearance of extant genera (the iguanids *Liolaemus* and *Pristidactylus* and the teiids *Tupinambis* and *Callopistes*). Late Early Miocene deposits provide materials of *Pristidactylus* and *Tupinambis*, whereas an indeterminate tupinambine of the Mid-Miocene is the youngest Neogene record of a lizard in Patagonia. Palaeoclimatic changes affected the distributional patterns of lizards in Patagonia, restricting the distribution of *Pristidactylus* and *Tupinambis*, which, during the Miocene, extended to localities more southern than at present. The uplift of the austral Andean cordillera would have been decisive for the diversification of *Liolaemus* and *Pristidactylus* on both sides the Andes, whereas the trans-Andean teiid *Callopistes* had a widespread distribution in the past, reaching the Pampean Region and Patagonia, in Argentina.

Keywords Iguania · Scincomorpha · Teiidae · Patagonia · Argentina · Cretaceous · Cenozoic

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A. M. Albino (✉)
CONICET – Departamento de Biología, Universidad Nacional de Mar del Plata,
Mar del Plata, Argentina
e-mail: aalbino@mdp.edu.ar

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6.1 Introduction

In spite of the presently high diversity of lizards in Patagonia, the fossil record is still scarce and discontinuous. Patagonian fossil lizards have been documented since the nineteenth century (Ameghino 1893, 1898, 1899). These records, and others made during the last century, have been summarized and interpreted in classic literature concerning the fossil herpetofauna of South America (Báez and Gasparini 1977, 1979; Estes 1983; Estes and Báez 1985; Gasparini et al. 1986; Albino 1996). These early revisions were based on restricted and chronologically sporadic records, and, in many cases, the specimens were only mentioned but the material had not been neither studied nor revised. More recently, new palaeontological explorations carried out in Argentina provided additional material from diverse localities and geological periods. At the same time, the development of a research project focused on the fossil squamates of South America allowed a more rigorous anatomical and taxonomic study of the old and new material. Partial modern reviews concerning Patagonian fossil lizards have been included in Albino (2011) and Albino and Brizuela (2014a, 2015). Although the record is still scarce, it provides valuable information concerning the origin and evolution of modern lizard taxa.

This chapter is an attempt to evaluate the information that the fossil record can provide about the historical evolution of lizards in Patagonia. For this compilation, the geographic and stratigraphic references were revised. In some cases, a discussion about the taxonomic allocation of the remains is provided. Thus, this chapter represents an updated systematic review of the available information for this reptile group in Mesozoic and Cenozoic Patagonia.

Institutional abbreviations are as follows: MACN A, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Colección Nacional Ameghino, Ciudad Autónoma de Buenos Aires, Argentina; MACN Pv, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Colección Nacional de Paleovertebrados, Ciudad Autónoma de Buenos Aires, Argentina; MLP, Museo de La Plata, Paleontología de Vertebrados, La Plata, Argentina; MPCA, Museo Provincial “Carlos Ameghino”, Cipolletti, Argentina; MPCN, Museo Patagónico de Ciencias Naturales, General Roca, Argentina; MPEF PV, Museo Paleontológico “Egidio Feruglio”, Paleontología de Vertebrados, Trelew, Argentina; and MPM PV, Museo Regional Provincial Padre Manuel Jesús Molina, Río Gallegos, Argentina.

6.2 The Restrictions of the Fossil Record

The squamates are relatively small animals with gracile skeletons that require an appropriate depositional environment for preservation in good conditions. Fine sediments and low energy produce relatively complete articulate skeletons, but these conditions are not frequent for many continental tetrapod-bearing beds of the Cretaceous and Cenozoic of Patagonia. Thus, squamate remains are usually obtained as a consequence of searching for large reptiles (Mesozoic) or mammals (Cenozoic) that are more numerous than squamates in Patagonian vertebrate deposits. During explorations to obtain fossil squamates, it is frequent to apply a suitable strategy to search for and pick up small bones. Matrix collected in bulk then macerated to produce a concentrate of isolated elements, followed by picking in the lab using a stereoscopic microscope, is the most common way to collect scattered remains of microvertebrates. This technique usually produces large numbers of remains of diverse taxa (fishes, amphibians, reptiles, birds, mammals), which give a more complete picture of the assemblage as a whole, but unfortunately, the recovered bones are disarticulated and, usually, broken. Many of the squamate remains obtained may be useless for taxonomic purposes due to the incomplete preservation, or they can be identified only at high taxonomic levels. Thus, only a small part of the collected sample will be identified. In spite of this, the resulting data are often useful in plotting distributions.

6.3 Geographical and Climatic Evolution of Patagonia

Modern-day Patagonia is the result of the interaction of global tectonics, sea level fluctuations and palaeogeographical and palaeoclimatic changes. These events were decisive in the changes that affected distribution patterns of lizards as well as for other taxa (Albino 2011; Albino and Brizuela 2014a, b, 2015). Because of this, a brief summary of the principal events in the geographical and climatic evolution of Patagonia, based on the detailed reconstruction of Iglesias et al. (2011) and Nullo and Combina (2011), is given here.

During the Cretaceous, along with the progressive breakup of Gondwana, the climate was much warmer than today, and temperate climate conditions extended even to the poles. The evolution of Patagonia was in part independent from the evolution of the rest of Gondwana because Patagonia remained connected to Antarctica for a long time facilitating the evolution of a fauna that was endemic of the South America-Antarctica island continent. The transformation process of Patagonia during the Cenozoic included two fundamental events: (1) the opening of the Drake Passage during the Eocene-Oligocene transition, which separated Antarctica from Patagonia and originated cooler conditions, and (2) the increase of the Andean activity during the Miocene, which obstructed the passage of the humid winds and generated a process of desertification (Chap. 3).

Climatically, the Palaeocene and Eocene were quite warm, with tropical conditions extending north and south towards the poles, 10° S beyond their current limit. By contrast, the Oligocene was characterized by cooling and aridity resulted from the development of a semi-permanent ice layer in Antarctica. During the Late Oligocene and the Early Miocene, a time of global warming produced a change to a warmer climate in the Patagonian region. The trend towards global cooling became marked during the Miocene, although with a short episode with increasing of temperatures during the Middle Miocene. After this climatic episode, there was another important cooling event. Late Miocene was characterized by the final demise of megathermal elements in Patagonia. Concomitantly with these changes, biomes moved from tropical forest to steppes, through a sequence comprising subtropical forests, woodland savanna, park savanna and grassland savanna.

6.4 Geochronological Context

The Neuquén Basin is perhaps the best-known sedimentary basin of Patagonia. Its Cretaceous terrestrial beds are some of the most fossiliferous and stratigraphically complete worldwide. In Argentina, it is exposed in the Provinces of Neuquén, Mendoza, Río Negro and La Pampa. The estimated ages of each unit that conforms the Neuquén Basin have been mainly obtained from the ages of the superimposed intervals limited by regional unconformities as a result of the tectonosedimentary evolution (Vergani et al. 1995). The Neuquén and Malargüe groups constitute the Upper Cretaceous strata of the Neuquén Basin (Fig. 6.1). They are separated from the previous strata by the Main Miranican unconformity (Leanza et al. 2004). The Neuquén Group was laid down during nearly 20 Ma from the Cenomanian (Candeleros Formation) through to the Campanian (Anacleto Formation) and is separated from the strata of the Malargüe group by the Huantraiquican unconformity (Fig. 6.1). Mesozoic lizards of Patagonia come only from the Candeleros and Anacleto formations.

With respect to the Cenozoic, land mammal ages are a widely used system to establish a time scale for terrestrial faunal record. Each land mammal age is characterized by one or more species of mammals (or a combination of species of

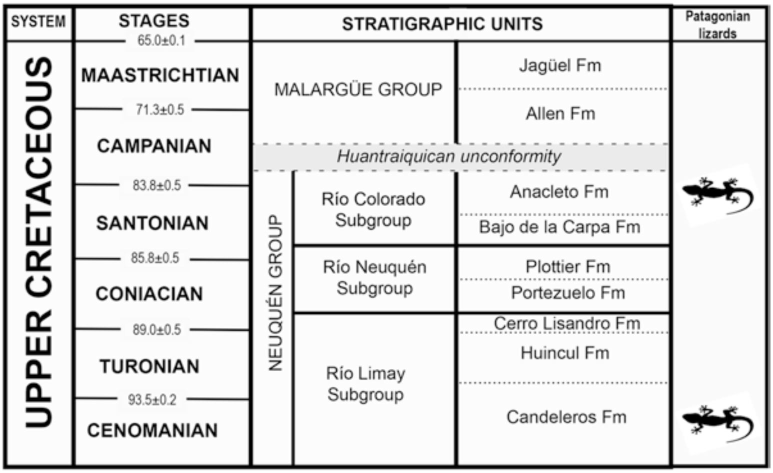


Fig. 6.1 Cretaceous stratigraphy of southern Neuquén Basin. Modified from Leanza et al. (2004)

mammals) that are unique for each period. By examining a large number of faunas of different ages, an entire time scale is erected based on the succession of mammal species. Each unit in the time scale is known as a land mammal age. In South America, most of the land mammal ages have traditionally been based on fossil localities of Patagonia. The biochronological context for the Cenozoic used in this chapter is then based on the South American Land Mammal Ages (SALMA, Pascual et al. 1996). The calibration used follows that given by Gelfo et al. (2009) and Woodburne et al. (2013) for the Patagonian Palaeogene, and Vucetich et al. (2007), Cione et al. (2007) and Cione and Báez (2007) for the remaining SALMAs (Fig. 6.2). Patagonian Cenozoic lizards come from deposits of the Deseadan, Colhuehuapian, Pinturan, Santacrucian and Colloncuran SALMAs.

6.5 Fossil Lizards of Patagonia

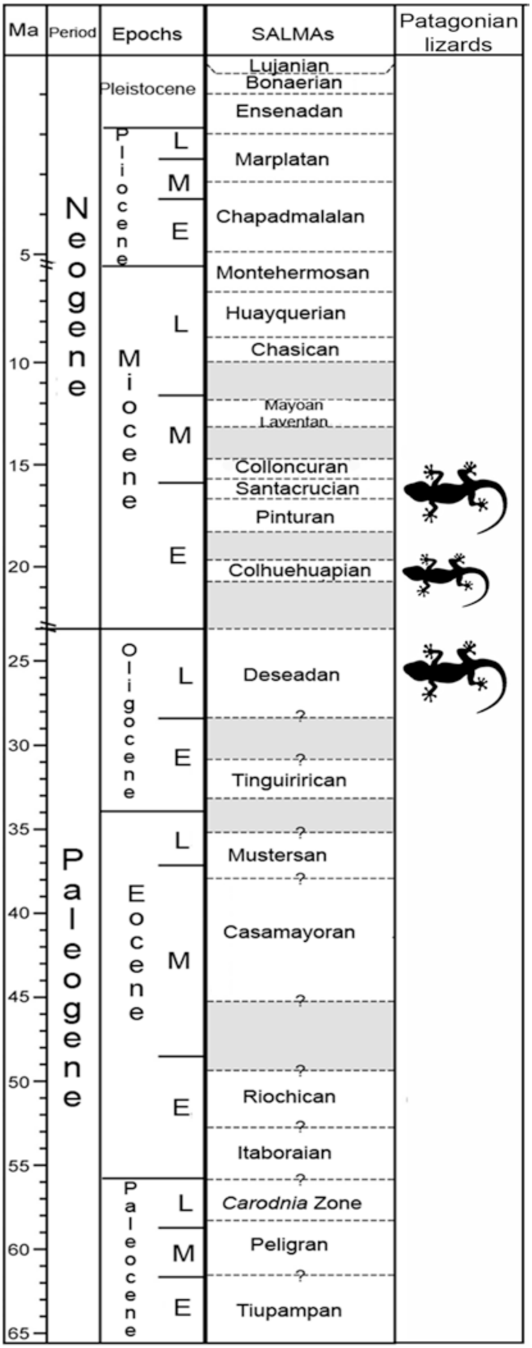
Few lizard species have been described so far for the Mesozoic of Gondwana, producing one of the largest palaeobiogeographical gaps in the knowledge of squamate evolution (Evans 2003). The known lizard diversity in the Mesozoic of South America is extremely restricted; thus, there is an important obstacle in knowing the origin and radiation of these squamates in southern territories.

Lizards first appeared in South America during the Early Cretaceous (Aptian-Albian) but they just became more frequent at the Cenozoic. Currently, only two main clades of lizards are present in the Mesozoic and Cenozoic record of Patagonia; they are Iguania and Scincomorpha. Both taxa emerged in this territory during the Upper Cretaceous.

Iguania Fragmentary remains recovered in Argentina and Brazil support the presence of Iguania in South America since the Mesozoic. The earliest of these records comprises nearly complete fused frontals (MPCA 250) encountered in rocks of the early Late Cretaceous of Patagonia (Apesteguía et al. 2005). The remain was collected in the upper layers of the Candeleros Formation (Cenomanian-Turonian) at the La Buitrera fossil quarry, Cerro Policía, Río Negro Province, northwestern Patagonia [Fig. 6.3 (1)].

The specimen was assigned to an iguanian (possibly Iguanidae) due to a combination of the following features (Apesteguía et al. 2005): (1) the frontals are fused in a sole bone, (2) it is strongly constricted between orbits giving hourglass shape and (3) it bears pronounced ornamentation. Daza et al. (2012) believe that the character combination listed by Apesteguía et al. (2005) is not exclusive to any lizard group whereas Albino and Brizuela (2014a) verify that the simultaneous presence of these characters is only observed in Iguanidae, considering valid the tentative assignation given by Apesteguía et al. (2005). Among Iguanidae, Apesteguía et al. (2005) suggested similarities in the dermal sculpturing with the extant Tropidurinae *Liolaemus*. However, Albino and Brizuela (2014a) noticed that the frontal exhibits well-developed supraorbital flanges, which, according to Smith (2009), are present

Fig. 6.2 Cenozoic time scale for South American Land Mammal Ages (SALMAs)



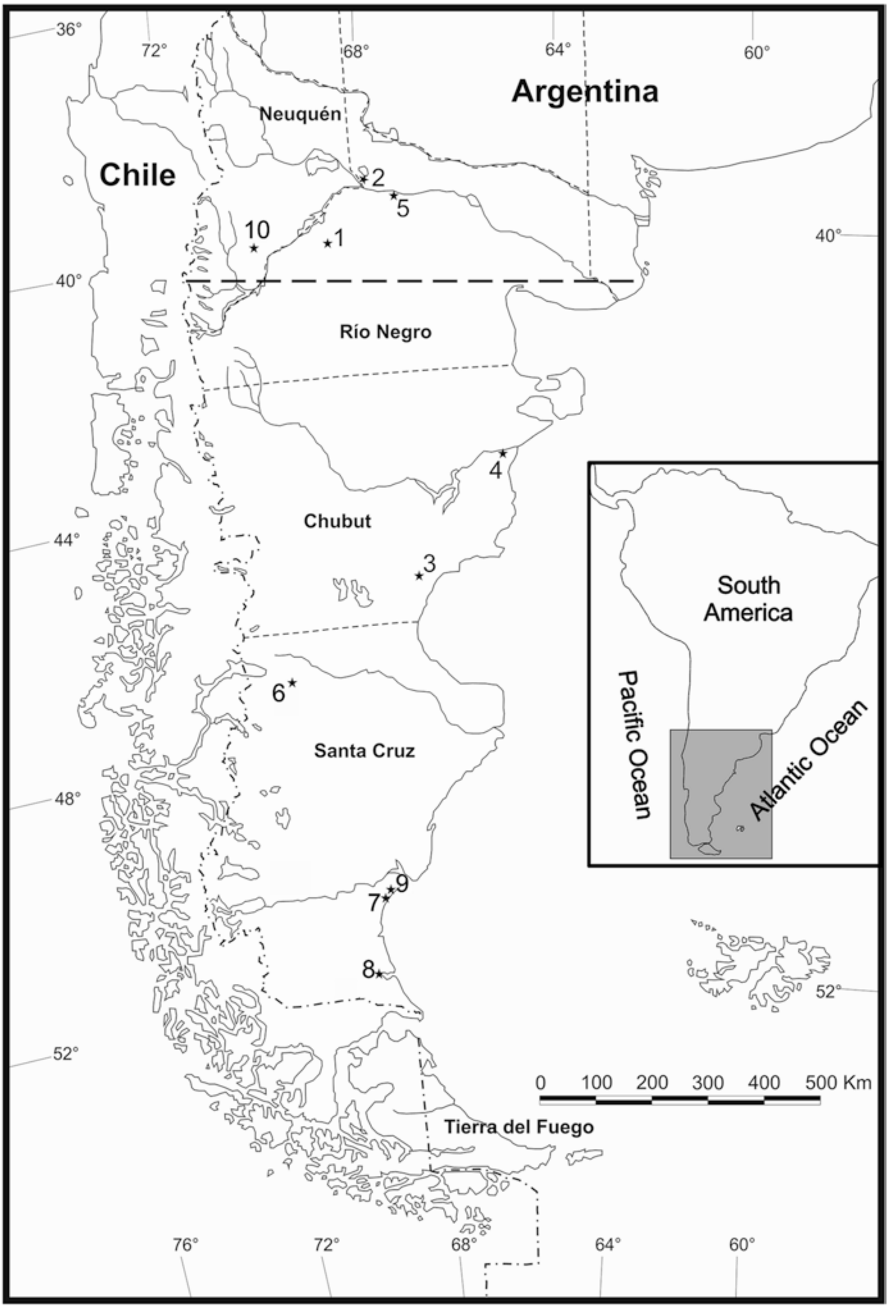


Fig. 6.3 Distribution of Patagonian fossil lizards: (*1*) La Buitrera (Apesteguía et al. 2005); (*2*) Cinco Saltos (Brizuela and Albino 2011); (*3*) Cabeza Blanca (Albino and Brizuela 2014b); (*4*) Gaiman (Albino 2008; Brizuela and Albino 2004); (*5*) Paso Córdova (Quadros et al. 2018); (*6*) Río Pinturas (pers. obs.); (*7*) La Cueva (Ameghino 1899; Albino et al. 2017); (*8*) Killik Aike Norte (Albino et al. 2017); (*9*) Monte León (Ameghino 1893; Brizuela and Albino 2008a; Albino et al. 2017); (*10*) Cañadón del Tordillo (Brizuela and Albino 2008b); the interrupted line shows the southern range limit of extant Tupinambinae

in Polychrotinae and Corytophaninae. These authors also observed that the dermal sculpturing morphology is similar to that of some Polychrotinae. Therefore, the Cretaceous specimen shows a possible Polychrotinae affinities, rather than to Tropidurinae (sensu Smith 2009).

Younger records of other non-acrodontan iguanians in the Upper Cretaceous of South America are represented by two extinct genera and species coming from Brazil: *Brasiliguana prudentis* from the Turonian-Santonian (Nava and Martinelli 2011) and *Pristiguana brasiliensis* from the Maastrichtian (Estes and Price 1973). Hence, the Patagonian specimen together with the species from Brazil supports the idea that, by the phase of the Laurasia-Gondwana division, the Iguania, and possibly the pleurodont Iguanidae clade, constituted already part of the herpetological communities of South America.

Indeterminate non-acrodontan dentaries were mentioned for the Campanian-Maastrichtian of Patagonia (Leanza et al. 2004; Albino 2007; Simões et al. 2017), but they have been recognized as recent remains (Albino 2011).

Later to the Upper Cretaceous, an Early Palaeocene dentary from the Tiupampan SALMA of Bolivia (Rage 1991) could be the earliest Iguanidae in the South American Cenozoic. A well-preserved mandible and a fragment of a maxilla reported for the Early Eocene (Itaboraian SALMA) of Brazil (Carvalho 2001) are consistent with the Mesozoic and Early Palaeocene record, supporting an ancient presence of Iguanidae in South America, but the material is not sufficiently well preserved to provide evidence of relationships with any current iguanid subfamily.

During a long time, the fossil record of Iguania in South America had an occurrence large gap between the Early Eocene and Early Miocene (Albino 2011; Albino and Brizuela 2014a). Recently, fossils found in levels attributed to the Late Oligocene of the Sarmiento Formation (Deseadan SALMA) at the locality of Cabeza Blanca, in Chubut Province [Fig. 6.3 (3)], partially fill this interval (Albino and Brizuela 2014b). The squamates recovered in this Patagonian site include two remains which belong to lizards: a tooth-bearing fragment appertaining to a maxilla or dentary (MPEF PV 1460) and an isolated presacral vertebra (MPEF PV 1463). The first was assigned to an indeterminate Iguanidae, whereas the latter probably belongs to an Iguaninae (Albino and Brizuela 2014b). Until the moment, no other Palaeogene iguanian was reported for South America.

For the Neogene, the Early Miocene fossil-bearing beds of the Sarmiento Formation at Gaiman [Fig. 6.3 (4)], in Chubut Province (Colhuehuapian SALMA), have provided one of the most relevant associations of South American fossil lizards where both iguanians and scincomorphs are present (Brizuela and Albino 2004; Albino 2008). Iguania are well represented by many fragmentary remains deposited in MPEF PV and MLP, most of them indeterminate at low taxonomic levels. Among the best-preserved specimens, dentaries and maxillae assigned to extant iguanian genera (*Pristidactylus* and *Liolaemus*) were recognized for first time (Albino 2008). The calibration of the Colhuehuapian SALMA was recently dated around 20–21 Ma (Dunn et al. 2013); this means that the mentioned genera are old components of the Patagonian lizard communities since they are presently diverse in this territory.

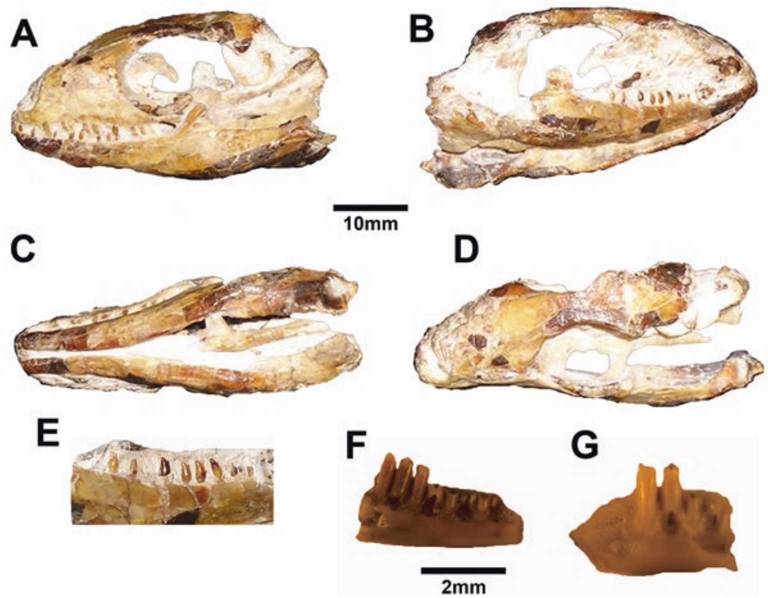


Fig. 6.4 (**a**–**e**) *Callopistes* from the early Miocene of Chichinales, skull in left (**a**), right (**b**), ventral (**c**) and dorsal (**d**) views; teeth of the right dentary (**e**); (**f**–**g**) fragmentary toothed remains of probable Iguania from the early Miocene of Río Pinturas

The Pinturan SALMA (Early Miocene) in Ea. Los Toldos, Río Pinturas, Santa Cruz Province [Fig. 6.3 (6)], provided highly fragmentary and undescribed remains (MACN-SC 316 and 317) of probable Iguania (Fig. 6.4, personal observation).

Iguanians have also been recognized in various Santacrucian sites (Albino 1996, 2011). In 1899, Florentino Ameghino erected the extinct iguanid genus *Erichosaurus* based on tooth-bearing remains recovered from sediments of the Santa Cruz Formation (Santacrucian SALMA) in the locality La Cueva, southeastern Santa Cruz Province [Fig. 6.3 (7)]. The age of the Santa Cruz Formation is currently estimated in about 18 to 16 Ma, corresponding to the late Early Miocene (Perkins et al. 2012). Ameghino (1899) described three species of *Erichosaurus* from this formation (*E. diminutus*, *E. bombimaxilla* and *E. debilis*), which Estes (1983) considered nomina dubia. A preliminary revision of the remains was made newly by Fernicola and Albino (2012), invalidating *Erichosaurus* and its species. The holotype of *Erichosaurus debilis* is represented by a right dentary articulated to the surangular (MACN A 5807), whereas that of *Erichosaurus diminutus* is a right maxilla (MACN A 2272). The specimens were at last redescribed by Albino et al. (2017), concluding that *E. debilis* and *E. diminutus* are indeterminate species of the extant polichrotine *Pristidactylus*. With respect to the holotype of *E. bombimaxilla*, it includes three fragments of toothed bones (MACN A 2283a, b and c) presumably corresponding to a right dentary of a single individual. It has been identified as an indeterminate iguanid (Albino et al. 2017). In addition, a new partial left hemimandible, including splenial and dentary (MPM PV 4337), was collected not long ago in Santacrucian levels of the locality Killik Aike Norte, the southernmost locality where Cenozoic lizards were found [Fig. 6.3 (8)]. It also corresponds to an indeterminate species of the genus *Pristidactylus* (Albino et al. 2017), but this species would be clearly different from that represented by the specimen MACN A 5807. Dimensions of the maxilla MACN A 2272 are not equivalent to those of neither MACN A 5807 nor MPM PV 4337, although this could be because it corresponds to a younger individual of one of these species (Albino et al. 2017).

Other reports of Iguania in Patagonia come from Quaternary archaeological sites of Mendoza (*Leiosaurus*) and Santa Cruz Provinces (*Liolaemus*) (Mengoni Goñalons and Silveira 1976; Van Devender 1977; Albino and Franco 2011; Albino 2017).

Scincomorpha Cretaceous lizard remains from Brazil and Argentina provide evidence about the presence of Scincomorpha in South America since the Mesozoic. The oldest scincomorph lizard is the recently described *Calanguban alamoi* from the Early Cretaceous of northeastern Brazil (Simões et al. 2014), which, together with *Tijubina pontei* (Bonfim-Júnior and Marques 1997) and *Olindalacerta brasiliensis* (Evans and Yabumoto 1998) from the same Crato Formation, represent the oldest squamates known to date in South America.

With respect to Patagonia, Brizuela and Albino (2011) have tentatively assigned a poorly preserved dentary from the Upper Cretaceous of northern Patagonia to the Scincomorpha. The material, badly preserved, comes from deposits of the Anacleto Formation at Cinco Saltos, Río Negro Province [Fig. 6.3 (2)]. This dentary reinforces the evidence given by *Calanguban* about the presence of Scleroglossa in the South American Cretaceous. Within the Scincomorpha, the Patagonian dentary shows affinities with the Scincoidea suggesting that Scincoidea-like lizards would have had Gondwanan distribution (Brizuela and Albino 2011).

Cenozoic South American scincomorphs also constitute part of the diverse, but undescribed, Itaboraian lizard fauna of Brazil (Carvalho 2001). They demonstrate that the principal clades of lizards probably were diversified in South America at least since the Early Eocene (Albino 2011). Early Eocene deposits of the Lumbrera Formation in northwestern Argentina (Salta Province) provided remains of an extinct teiid lizard (Tupinambinae, *Lumbrerasaurus scagliai*) corroborating the presence of scincomorphs in the Palaeogene (Brizuela and Albino 2016). In spite of this early record, scincomorphs are completely absent from the Palaeogene of Patagonia.

In contrast with the Palaeogene, Neogene deposits of Patagonia are relatively fertile in scincomorph remains, including extant genera of teiids. Early Miocene deposits of Gaiman [Chubut Province, Fig. 6.3 (4)] and Chinchinales [Río Negro Province, Fig. 6.3 (5)], provided relevant Colhuehuapian lizard remains that include the genera *Tupinambis* and *Callopistes*, respectively (Fig. 6.4) (Brizuela and Albino 2004; Quadros et al. 2018). These records support the minimum age of origin of both genera in ~20–21 Ma. Brizuela and Albino (2004) first described remains attributed to *Tupinambis* based on fragmentary dentaries and maxillae deposited in the MACN Pv, whereas the articulated skull assigned to *Callopistes* is placed in the MPCN.

In 1893, Florentino Ameghino named two reptilian taxa for three small, fragmentary jaws from the Miocene of southeastern Argentina ("*Diasemosaurus occidentalis*" and "*Dibolosodon typicus*"), but he never described the specimens in detail or figured them. The remains had been discovered in Monte León locality [Fig. 6.3 (9)], in deposits currently considered belonging to the Santacrucian SALMA (late Early Miocene). Brizuela and Albino (2008a) redescribed these specimens and identified them as fossil dentaries (MACN A 621 and MACN A 5806-a) and a maxilla (MACN A 5806-b) of an indeterminate species of the extant teiid *Tupinambis*. They constitute the southernmost records of teiids.

Deposits from the Colloncuran (Mid-Miocene) at Cañadòn del Tordillo, near Piedra del Águila [Neuquén Province, Fig. 6.3 (10)], also contributed with remains of a teiid Tupinambine (*Tupinambis* sp. or *Crocodilurus* sp., Brizuela and Albino 2008b). Excluding the iguanian specimens coming from archaeological sites, the Colloncuran remains constitute the youngest fossil record of lizards in Patagonia.

6.6 Origin and Evolution of the Lizard Fauna of Patagonia Based on the Fossil Record

In 1983, Richard Estes proposed a hypothesis about the early evolution of lizards in which the separation of Laurasia and Gondwana during the Jurassic produced northern populations of scleroglossans and southern ones of iguanians. As a result of the breakup of Gondwana, South America and Antarctica formed an independent island continent that was isolated to the north and east by oceans. According to Presch (1974), Estes (1983) and Estes and Báez (1985), a short terrestrial connection between North America and northern South America occurred during the Upper Cretaceous, permitting migration of vertebrates in both senses; thus, iguanians would have migrated to the North whereas scleroglossans (teiioids) to the South. Recent discoveries suggest that the earliest radiation of Iguania, and then the separation of Iguania and Scleroglossa, could have taken place at least at the end of the Triassic, before the fragmentation of the Pangaean supercontinent (Evans 2003). Based on the fossil record detailed here, it is possible to support the idea that the Iguania inhabited South America and, in particular, Patagonia, as early as by the phase of the Laurasia-Gondwana division. The Early Cretaceous South American lizard *Calanguban* suggests that scincomorphs were already present in this continent during the Aptian/Albian. In addition, the discovery of an acrodontan lizard (*Gueragama sulamericana*) in the Turonian-Campanian of Brazil provides evidence that a group of lizards, which is entirely absent in South America today, occurred in this continent back in the Cretaceous (Simões et al. 2017). This whole scenario suggests that the pattern of distribution of daughter lineages on Laurasia and Gondwana was probably far more complex than imagined. Thus, future discoveries of South

American fossil lizards could provide better evidence in relation to the early diversification of squamates.

As already mentioned, during the Cretaceous there was a global climatic condition much warmer than today, geographically uniform and extended to the poles (Nullo and Combina 2011). Favoured by the temperate climate conditions, relatively large-bodied snakes were frequent components of the Patagonian Cretaceous herpetofauna (Albino and Brizuela 2014a), whereas both iguanians and scincomorphs lizards, found in the same deposits that some of these snakes, were of small size. Presumably, other reptiles, as sphenodonts and dinosaurs, which were numerous and represented by a huge diversity of forms (Leanza et al. 2004), occupied the niches appropriate for large-bodied lizards. This would explain the absence of large lizards in the Patagonian Cretaceous.

For the Late Palaeogene, the presence of an Iguaninae at a latitude of 45° S in the late Oligocene of Patagonia (Albino and Brizuela 2014b) is unexpected because these lizards are presently absent from the Argentine territory. Extant Iguaninae are mainly distributed from United States through Central America and the Caribbean, reaching Brazil and Paraguay in South America; hence, the iguanine recovered in the Patagonian Palaeogene greatly exceeds the present range of distribution of the group. This could be explained considering that a global warming event occurred during the Late Oligocene (Nullo and Combina 2011) potentially extending the climatological conditions necessary to support thermal requirements of the iguanines and thus allowing their presence as south as Patagonia. Iguanines are known from the Late Eocene of North America at equivalent mid-latitudes (46° N) supporting a greater distribution in the Palaeogene in comparison to the present day (Albino and Brizuela 2014b).

With respect to the Neogene, Colhuehuapian lizards of Patagonia include earliest records of extant genera of Iguanidae (*Liolaemus*, *Pristidactylus*) and Teiidae (*Tupinambis*, *Callopistes*). At least two of these genera (*Pristidactylus* and *Tupinambis*) were also recorded for the Santacrucian. At present, iguanids inhabit as south as the Tierra del Fuego Island (Cei 1986). The material from the Santacrucian represents the southernmost fossil records of lizards in South America and indicates that iguanids distributed in southern Patagonia as back as the late Early Miocene (Albino et al. 2017).

According to data regarding present distribution of *Liolaemus* and *Pristidactylus* in Patagonia (Breitman et al. 2014; Minoli et al. 2015), the Miocene record of *Liolaemus* at the locality of Gaiman, in Chubut Province, does not contrast with its current range of distribution, whereas the fossil record of *Pristidactylus* is rather southern that at the present time. In Argentina, six species of *Pristidactylus* are distributed in disjunct areas over a 29° to 45° S latitudinal range (Minoli and Avila 2011). The Early Miocene distribution of the genus in Gaiman locality does not coincide with the reported present distribution of the genus in this department, although it has been recognized at such latitudes (43° S) and up to the northernmost limit of the Santa Cruz Province (46° S) (Minoli and Avila 2011; Avila et al. 2018). The late Early Miocene record of the genus in southern Santa Cruz Province (beyond the 50° S) implies a more widespread range of dispersion to the south (Albino et al. 2017).

Tupinambine teiids, and especially the genus *Tupinambis*, also have a past distribution extended beyond the current limit that is at the 40° S (Fig. 6.3). They reached the 43° S during the Colhuehuapian (Brizuela and Albino 2004), whereas they approximately reached the 50° S and 70° W during the Santacrucian and Colloncuran, respectively (Brizuela and Albino 2008a, b). Therefore, the distributional range of both *Pristidactylus* and the tupinambines during the Early Miocene could be explained taking into account the warm conditions developed at this time as far as southern Patagonia, from the incipient eastern slopes of the Andes to the Atlantic coast. These conditions would have extended at least until the Mid-Miocene. The progressive decrease in temperatures through the Middle–Late Miocene and later (Nullo and Combina 2011) would have caused the restriction in the distribution of *Pristidactylus* and tupinambine teiids to environments with more temperate climates (Albino 2008, 2011; Brizuela and Albino 2004, 2008b; Albino and Brizuela 2014a, 2015). The present southernmost population of *Tupinambis rufescens* in northern Patagonia (Cei and Scolaro 1982) is likely a relic of its broader distribution. The distribution and diversity of *Pristidactylus* at both sides of the Andes (Minoli and Avila 2011) probably were determined by the elevation of the Andean cordillera during the Miocene, producing subsequent vicariance events, as it was the case for the genus *Liolaemus* (Albino 2008).

The cooling after the Miocene Climatic Optimum event in southern South America was accompanied with the retreat of an important marine transgression ("Mar Paranaense") and the uplift of the Andes (Quechua phase) which gave way to the "Edad de las Planicies Australes" during the Late Miocene–Early Pliocene (Pascual et al. 1996). In Patagonia, the climate became cooler and the vegetation was similar to the present, with the steppe expanding across extra-Andean Patagonia, and the forest restricted to the westernmost areas where rainfall was still abundant (Nullo and Combina 2011). Unfortunately, fossil records of Patagonian lizards after the Colloncuran are so far absent.

With respect to the tupinambine teiid *Callopistes*, the current presence of the two extant species *Callopistes flavipunctatus* and *C. maculatus* is restricted to a trans-Andean distribution, throughout Chile, Peru and Southern Ecuador. The unique described fossil remains of the genus came from the Montehermosan SALMA (Late Miocene–Early Pliocene) in southeastern Buenos Aires Province, on the Atlantic coast of Argentina. This record corresponds to the extinct species *Callopistes bicuspidatus* (Chani 1976; Brizuela and Albino 2017). Recently, a new fossil record of the genus was reported for the Colhuehuapian of Patagonia (Quadros et al. 2018) confirming that *Callopistes* had a much broader distribution in the past, reaching cis-Andean areas of the Pampean Region and Patagonia. Molecular data indicate that *Callopistes* would have diverged from all other Tupinambinae during the Palaeocene (Giugliano et al. 2007). The uplift of the mountain system during the Miocene could have caused the divergence of the species at both sides of the Andes (Brizuela and Albino 2017). The present distribution and diversity of the genus is therefore relictual.

6.7 Conclusions

The fossil record of squamates in Patagonia is still scarce but it represents one of the most prolific of entire South America. Observation of the current fossil record reveals that some taxa comprising the present Patagonian herpetofauna have a considerable antiquity in this region. The presence of lizards in Patagonia extends back as far as the Late Mesozoic.

The Patagonian Mesozoic record of lizards gives a noticeable contrast to the pattern of conservation of snakes, which produced exquisitely preserved skeletons that provide relevant phylogenetic information about the origin and basal evolution of the clade (Albino and Brizuela 2014a, 2015). The deposits where snakes have been recovered but lizards have not are also rich in medium- to large-bodied vertebrate taxa as crocodiles, dinosaurs and birds (Leanza et al. 2004). Taking into account that lizards are usually recovered in Mesozoic deposits of other territories, especially of Laurasia (Evans 2003), the scarcity of lizard remains in the Patagonian Mesozoic could be consequence of a combination of two factors: the small size of the specimens that inhabited Patagonia and the unusual presence of lizards in the vertebrate communities of this region. Nevertheless, the presence of both iguanians and scincomorphs in the Patagonian Cretaceous, together with the Brazilian Mesozoic record, reveal that South America would have played an important, and still unknown, role in the early diversification of squamates.

Two fundamental gaps currently exist in the lizard fossil record of Patagonia: one is from the Late Cretaceous (Anacleto Formation) to the Late Oligocene (at least 50 million years), and the other is from the Mid-Miocene to the Holocene (Figs. 6.1 and 6.2). The Mesozoic is poorly sampled by comparison with the Cenozoic. Therefore, the record is not complete enough to give a reliable picture of the evolution of lizards in Patagonia. The Miocene interval has produced most of the taxonomically informative fossil remains, including present-day taxa as the genera *Liolaemus*, *Pristidactylus*, *Tupinambis* and *Callopistes*.

Palaeoclimatic and palaeoenvironmental changes affected the distributional patterns of lizards in Patagonia. The trend towards global cooling from the Mesozoic to the Late Miocene, and the changes of biomes from tropical forests to steppes, would have affected the Patagonian lizard fauna restricting to the north the distribution of *Pristidactylus* and *Tupinambis* that reached the southernmost localities during the Early Miocene. Palaeogeographical changes, especially the uplift of the Andes, would have conditioned the occurrence of vicariance events with subsequent diversification at both sides of the Andes in *Liolaemus* and *Pristidactylus*, whereas unknown event(s) caused the disappearance of *Callopistes* east of the Andes, which signify a decreasing of its diversity.

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Chapter 7
Naming the Diversity: Taxonomy of Current Species of Patagonian Lizards

Luciano J. Avila, Andrea González Marín, Jaime Troncoso-Palacios, Kevin Imanol Sánchez, Cristian Hernán Fulvio Pérez, and Mariana Morando

Abstract The diversity of the Patagonian lizard fauna is a combination of low diversity at higher levels, e.g., families, some of them almost marginal to the region, coupled with very high species diversity concentrated in two genera *Liolaemus* and *Phymaturus*, and a high number of endemics. The number of described species almost tripled since Cei's last and only monograph on Patagonian herpetofauna in 1987. But changes were not limited to species numbers; taxonomy changed as studies of this fauna improved with the use of modern taxonomic techniques and dedicated field surveys made to some previously unknown areas. The purpose of this chapter is to provide a taxonomic summary of Patagonian lizards. We include a number of plates with pictures of poorly known and/or endemic Patagonian species probably never included in any book or publication.

Keywords Taxonomy · Species description · Species diversity · Systematics · Liolaemidae · Leiosauridae · Phyllodactylidae · Teiidae · Tropiduridae · Amphisbaenidae

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L. J. Avila (✉) · A. González Marín · K. I. Sánchez · M. Morando
Instituto Patagónico para el Estudio de los Ecosistemas Continentales – Consejo Nacional de Investigaciones Científicas y Técnicas (IPEEC-CONICET),
Puerto Madryn, Chubut, Argentina
e-mail: avila@cenpat-conicet.gob.ar; gmain@cenpat-conicet-gob.ar

J. Troncoso-Palacios
Programa de Fisiología y Biofísica, Facultad de Medicina, Universidad de Chile,
Santiago, Chile

C. H. F. Pérez
UAT, CCT-CONICET CENPAT, Puerto Madryn, Chubut, Argentina

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7.1 Diversity of the Lizard Fauna of Patagonia

Diversity of the Patagonian lizard fauna combines low diversity at higher levels, e.g., families, some of them almost marginal to the region, with a very high species diversity in the sister genera *Liolaemus* and *Phymaturus*. Including amphisbaenians, there are a total of six families of lizards distributed in the area covered by this book: Liolaemidae, Leiosauridae, Teiidae, Phyllodactylidae, Tropiduridae, and Amphisbaenidae. The Chilean Andes include only the Liolaemidae (Liolaemini) and Leiosauridae. We reviewed literature and scientific collections to obtain locality data, and included as part of the lizard fauna only species with at least one confirmed and vouchered record within the geographic boundaries of this study area. We provide an updated list of the species while avoiding discussions of taxonomic, systematic, nomenclatural or phylogenetic issues, but we include references about some species recognition problems.

The first comprehensive general publications including lizards of Patagonia are the now outdated books by Donoso-Barros (1966), and Cei's (1986) monograph, but since then more than 250 scientific articles, notes, technical reports, general field guides, or unpublished PhD theses have added information about lizards of this region. All information collection for this chapter was stopped on August 1, 2019.

A total of 169 species are included in this review (Tables 7.1 and 7.2), of which 159 belong to two families, Liolaemidae (Liolaemini) and Leiosauridae (Leiosaurae) (Fig. 7.1). The number of species restricted to Patagonia is high (Fig. 7.2a), and 93% of the Patagonian endemism can be attributed to *Liolaemus* and *Phymaturus* (Fig. 7.2b). Figure 7.2c shows endemic proportions by genera. Some species could be synonyms of other species based on some studies (e.g., Morando et al. 2003; Breitman et al. 2013; Avila et al. 2015a; Medina et al. 2017, 2018; Troncoso-Palacios et al. 2016b, 2018a, b), but our criteria were to only

Table 7.1 Families, genera, and species described for each genera following The Reptile Database (Uetz et al. 2019) and number of species found in the area covered by this book

Family	Genera	Number of species described	Number of species in the region covered by this book
Amphisbaenidae	*Amphisbaena*	96	2
Phyllodactylidae	*Homonota*	13	3
Teiidae	*Teius*	3	2
	Aurivela	2	1
	Salvator	3	1
Tropiduridae	*Stenocercus*	68	1
Leiosauridae	*Leiosaurus*	4	1
	Diplolaemus	4	4
	Pristidactylus	10	4
Liolaemidae	*Liolaemus*	265	113
	Phymaturus	48	37

Table 7.2 List of species included in this book, with descriptors and year of description

Family	Genus	Species	Author	Year	Subgenera
Amphisbaenidae	*Amphisbaena*	*kingii*	Bell	1833	
		plumbea	Gray	1872	
Teiidae	*Aurivela*	*longicauda*	Bell	1843	
	Salvator	*rufescens*	Günther	1871	
	Teius	*oculatus*	D'Orbigny, Bibron	1837	
		teyou	Daudin	1802	
Leiosauridae	*Diplolaemus*	*darwinii*	Bell	1843	
		leopardinus	Werner	1898	
		bibronii	Bell	1843	
		sexcinctus	Cei, Scolaro, Videla	2003	
	Pristidactylus	*araucanus*	Gallardo	1964	
		fasciatus	D'Orbigny, Bibron	1837	
		nigroiugulus	Cei, Scolaro, Videla	2001	
		torquatus	Philippi	1861	
	Leiosaurus	*bellii*	Duméril, Bibron	1837	
Tropiduridae	*Stenocercus*	*pectinatus*	Duméril, Bibron	1837	
Phyllodactylidae	*Homonota*	*darwinii*	Boulenger	1885	
		horrida	Burmeister	1861	
		underwoodi	Kluge	1964	
Liolaemidae	*Liolaemus*	*abdalai*	Quinteros	2012	*Liolaemus*
		antonietae	Troncoso-Palacios, Esquerré, Urra, Díaz, Castro-Pastene, Ruiz	2018	*Liolaemus*
		antumalguen	Avila, Morando, Pérez, Sites	2010	*Liolaemus*
		araucaniensis	Müller, Hellmich	1932	*Liolaemus*
		archeforus	Donoso-Barros, Cei	1971	*Eulaemus*
		austromendocinus	Cei	1974	*Liolaemus*
		avilae	Breitman, Parra, Pérez, Sites	2011	*Eulaemus*
		baguali	Cei, Scolaro	1983	*Eulaemus*
		brattstroemi	Donoso-Barros	1961	*Liolaemus*
		bibronii	Bell	1843	*Liolaemus*
		boulengeri	Koslowsky	1898	*Eulaemus*
		buergeri	Werner	1907	*Liolaemus*
		burmeisteri	Avila, Pérez, Medina, Sites, Morando	2012	*Liolaemus*
		calliston	Avila, Pérez, Minoli, Medina, Sites, Morando	2017	*Eulaemus*
		camarones	Abdala, Díaz-Gómez, Juárez-Heredia	2012	*Eulaemus*
		canqueli	Cei	1975	*Eulaemus*

(continued)

Table 7.2 (continued)

Family	Genus	Species	Author	Year	Subgenera
		caparensis	Breitman, Pérez, Parra, Morando, Sites, Avila	2011	*Eulaemus*
		carlosgarini	Esquerré, Nuñez, Scolaro	2013	*Liolaemus*
		casamiquelai	Avila, Pérez, Morando, Sites	2010	*Eulaemus*
		ceii	Donoso-Barros	1971	*Liolaemus*
		chacabucoense	Núñez, Scolaro	2009	*Eulaemus*
		chehuachekenk	Avila, Morando, Sites	2008	*Eulaemus*
		chiliensis	Lesson	1830	*Liolaemus*
		chillanensis	Müller, Hellmich	1932	*Liolaemus*
		choique	Abdala, Quinteros, Scrocchi, Stazzonelli	2010	*Liolaemus*
		coeruleus	Cei, Ortiz	1983	*Liolaemus*
		confusus	Núñez, Pincheira-Donoso	2006	*Liolaemus*
		crandalli	Avila, Medina, Pérez, Sites, Morando	2013	*Liolaemus*
		cristiani	Núñez, Navarro, Loyola	1991	*Liolaemus*
		curicensis	Müller, Hellmich	1938	*Liolaemus*
		curis	Núñez, Labra	1985	*Liolaemus*
		cuyanus	Cei, Scolaro	1980	*Eulaemus*
		cuyumhue	Avila, Morando, Pérez, Pérez, Sites, Morando	2009	*Eulaemus*
		cyaneinotatus	Martínez, Avila, Pérez, Sites, Morando	2011	*Liolaemus*
		cyanogaster	Duméril, Bibron	1837	*Liolaemus*
		darwinii	Bell	1843	*Eulaemus*
		donosobarrosi	Cei	1974	*Eulaemus*
		duellmani	Cei	1978	*Eulaemus*
		dumerili	Abdala, Semham, Moreno Azocar, Bonino, Paz, Cruz	2012	*Eulaemus*
		elongatus	Koslowsky	1896	*Liolaemus*
		escarchadosi	Scolaro, Cei	1997	*Eulaemus*
		exploratorum	Cei, Williams	1984	*Liolaemus*
		fitzingerii	Duméril, Bibron	1837	*Eulaemus*
		flavipiceus	Cei, Videla	2003	*Liolaemus*
		gallardoi	Cei, Scolaro	1982	*Eulaemus*
		goetschi	Müller, Hellmich	1932	*Eulaemus*
		gracilis	Bell	1843	*Liolaemus*

(continued)

Table 7.2 (continued)

Family	Genus	Species	Author	Year	Subgenera
		gravenhorstii	Gray	1843	*Liolaemus*
		grosseorum	Etheridge	2001	*Eulaemus*
		gununakuna	Avila, Pérez, Morando, Sites	2004	*Liolaemus*
		hatcheri	Stejneger	1909	*Eulaemus*
		hermannunezi	Pincheira-Donoso, Scolaro, Schulte	2007	*Eulaemus*
		inacayali	Abdala	2003	*Eulaemus*
		janequeoae	Troncoso-Palacios, Díaz, Púas, Riveros-Riffo, Elorza	2016	*Liolaemus*
		josei	Abdala	2005	*Eulaemus*
		kingii	Bell	1843	*Eulaemus*
		kriegi	Müller, Hellmich	1939	*Liolaemus*
		kolengh	Lobo, Abdala	2006	*Eulaemus*
		leftrarui	Troncoso-Palacios, Díaz, Púas, Riveros-Riffo, Elorza	2016	*Liolaemus*
		lemniscatus	Gravenhorst	1837	*Liolaemus*
		lentus	Gallardo	1966	*Eulaemus*
		lineomaculatus	Boulenger	1885	*Eulaemus*
		loboi	Abdala	2003	*Eulaemus*
		lonquimayensis	Escobar-Huerta, Santibañez Toro, Ortiz	2015	*Liolaemus*
		magellanicus	Hombron, Jacquinot	1847	*Eulaemus*
		mapuche	Abdala	2002	*Eulaemus*
		martorii	Abdala	2003	*Eulaemus*
		melanops	Burmeister	1888	*Eulaemus*
		monticola	Müller, Hellmich	1932	*Liolaemus*
		morandae	Breitman, Parra, Pérez, Sites	2011	*Eulaemus*
		morenoi	Etheridge, Christie	2003	*Eulaemus*
		multimaculatus	Duméril, Bibron	1837	*Eulaemus*
		neuquensis	Müller, Hellmich	1939	*Liolaemus*
		nitidus	Wiegmann	1834	*Liolaemus*
		parthenos	Abdala, Baldo, Juárez, Espinoza	2016	*Eulaemus*
		petrophilus	Donoso-Barros, Cei	1971	*Liolaemus*
		pictus	Duméril, Bibron	1837	*Liolaemus*
		puelche	Avila, Morando, Pérez, Sites	2007	*Eulaemus*
		punmahuida	Avila, Pérez, Morando	2003	*Liolaemus*

(continued)

Table 7.2 (continued)

Family	Genus	Species	Author	Year	Subgenera
		purul	Abdala, Semham, Moreno Azocar, Bonino, Paz, Cruz	2012	*Eulaemus*
		quinterosi	Ruiz, Quipildor, Bulacios Arroyo, Chafrat, Abdala	2019	*Liolaemus*
		rabinoi	Cei	1974	*Eulaemus*
		riodamas	Esquerré, Núñez, Scolaro	2014	*Liolaemus*
		rothi	Koslowsky	1898	*Eulaemus*
		sagei	Etheridge, Christie	2003	*Eulaemus*
		sarmientoi	Donoso-Barros	1973	*Eulaemus*
		shehuen	Abdala, Díaz-Gómez, Juárez-Heredia	2012	*Eulaemus*
		shitan	Abdala, Quinteros, Scrocchi, Stazzonelli	2010	*Liolaemus*
		schroederi	Müller, Helmich	1938	*Liolaemus*
		scolaroi	Pincheira-Donoso, Núñez	2005	*Eulaemus*
		scorialis	Troncoso-Palacios, Díaz, Esquerre, Urra	2015	*Liolaemus*
		senguer	Abdala	2005	*Eulaemus*
		septentrionalis	Pincheira-Donoso, Núñez	2005	*Liolaemus*
		sitesi	Avila, Olave, Pérez, Pérez, Morando	2013	*Eulaemus*
		smaug	Abdala, Quinteros, Scrocchi, Stazzonelli	2010	*Liolaemus*
		somuncurae	Cei, Scolaro	1981	*Eulaemus*
		silvanae	Donoso-Barros, Cei	1971	*Eulaemus*
		tari	Scolaro, Cei	1997	*Eulaemus*
		tehuelche	Abdala	2003	*Eulaemus*
		telsen	Cei, Scolaro	1999	*Eulaemus*
		tenuis	Duméril, Bibron	1837	*Liolaemus*
		thermarum	Videla, Cei	1996	*Liolaemus*
		tirantii	Avila, Pérez, Minoli, Medina, Sites, Morando	2017	*Eulaemus*
		tregenzai	Pincheira-Donoso, Scolaro	2007	*Liolaemus*
		tristis	Scolaro, Cei	1997	*Eulaemus*
		tromen	Abdala, Semham, Moreno Azocar, Bonino, Paz, Cruz	2012	*Eulaemus*

(continued)

Table 7.2 (continued)

Family	Genus	Species	Author	Year	Subgenera
		uptoni	Scolaro, Cei	2006	*Eulaemus*
		villaricensis	Müller, Hellmich	1932	*Liolaemus*
		wiegmannii	Duméril, Bibron	1837	*Eulaemus*
		xanthoviridis	Cei, Scolaro	1980	*Eulaemus*
		yatel	Abdala, Procopio, Stellatelli, Travaini, Rodríguez, Ruiz Monachesi	2014	*Eulaemus*
		zabalai	Troncoso-Palacios, Díaz, Esquerré, Urra	2015	*Liolaemus*
		zullyae	Cei, Scolaro	1996	*Eulaemus*
	Phymaturus	*cacivioi*	Lobo, Nenda	2015	*patagonicus*
		camilae	Scolaro, Jara, Pincheira-Donoso	2013	*patagonicus*
		calcogaster	Scolaro, Cei	2003	*patagonicus*
		castillensis	Scolaro, Pincheira-Donoso	2010	*patagonicus*
		ceii	Scolaro, Ibargüengoytia	2007	*patagonicus*
		curivilcun	Scolaro, Corbalán, Tappari, Obregón Streitenberger	2016	*patagonicus*
		damasense	Troncoso-Palacios, Lobo	2012	*palluma*
		delheyi	Avila, Pérez, Pérez, Morando	2011	*patagonicus*
		desuetus	Scolaro, Tappari	2009	*patagonicus*
		dorsimaculatus	Lobo, Quinteros	2005	*palluma*
		excelsus	Lobo, Quinteros	2005	*patagonicus*
		felixi	Lobo, Abdala, Valdecantos	2010	*patagonicus*
		etheridgei	Lobo, Abdala, Valdecantos	2010	*patagonicus*
		indistinctus	Cei, Castro	1973	*patagonicus*
		loboi	Troncoso-Palacios, Ferri-Yáñez, Laspiur, Aguilar	2018	*palluma*
		manuelae	Scolaro, Ibargüengoytia	2008	*patagonicus*
		maulense	Núñez, Veloso, Espejo, Veloso, Cortes, Araya	2010	*palluma*
		nevadoi	Cei, Castro	1973	*patagonicus*
		palluma	Molina	1782	*palluma*
		patagonicus	Koslowsky	1898	*patagonicus*

(continued)

Table 7.2 (continued)

Family	Genus	Species	Author	Year	Subgenera
		payuniae	Cei, Castro	1973	*patagonicus*
		querque	Lobo, Abdala, Valdecantos	2010	*palluma*
		rahuensis	González Marín, Pérez, Minoli, Morando, Avila	2016	*patagonicus*
		roigorum	Lobo, Abdala	2007	*palluma*
		sinervoi	Scolaro, Méndez de la Cruz, Ibargüengoytia	2012	*patagonicus*
		sitesi	Avila, Pérez, Pérez, Morando	2011	*patagonicus*
		somuncurensis	Cei, Castro	1973	*patagonicus*
		spectabilis	Lobo, Quinteros	2005	*patagonicus*
		spurcus	Barbour	1921	*patagonicus*
		tenebrosus	Lobo, Quinteros	2005	*patagonicus*
		timi	Hibbard, Nenda, Lobo	2019	*palluma*
		tromen	Lobo, Nenda	2015	*palluma*
		verdugo	Cei, Videla	2003	*palluma*
		videlai	Scolaro, Pincheira-Donoso	2010	*patagonicus*
		vociferator	Pincheira-Donoso	2004	*palluma*
		yachanana	Avila, Pérez, Minoli, Morando	2014	*patagonicus*
		zapalensis	Cei, Castro	1973	*patagonicus*

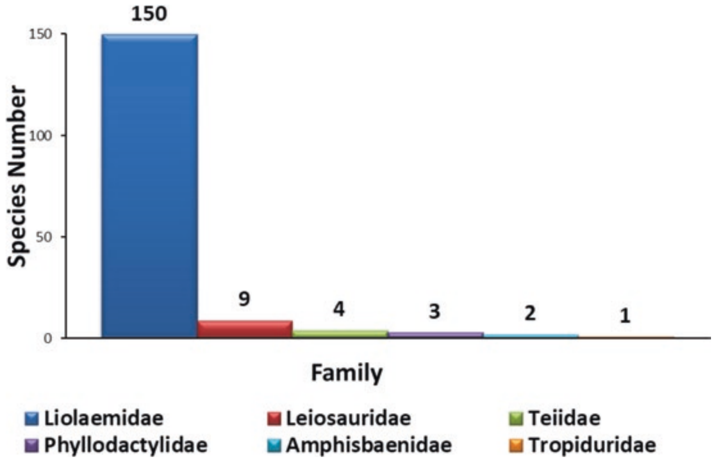

Fig. 7.1 Number of species of lizards by family in Patagonia

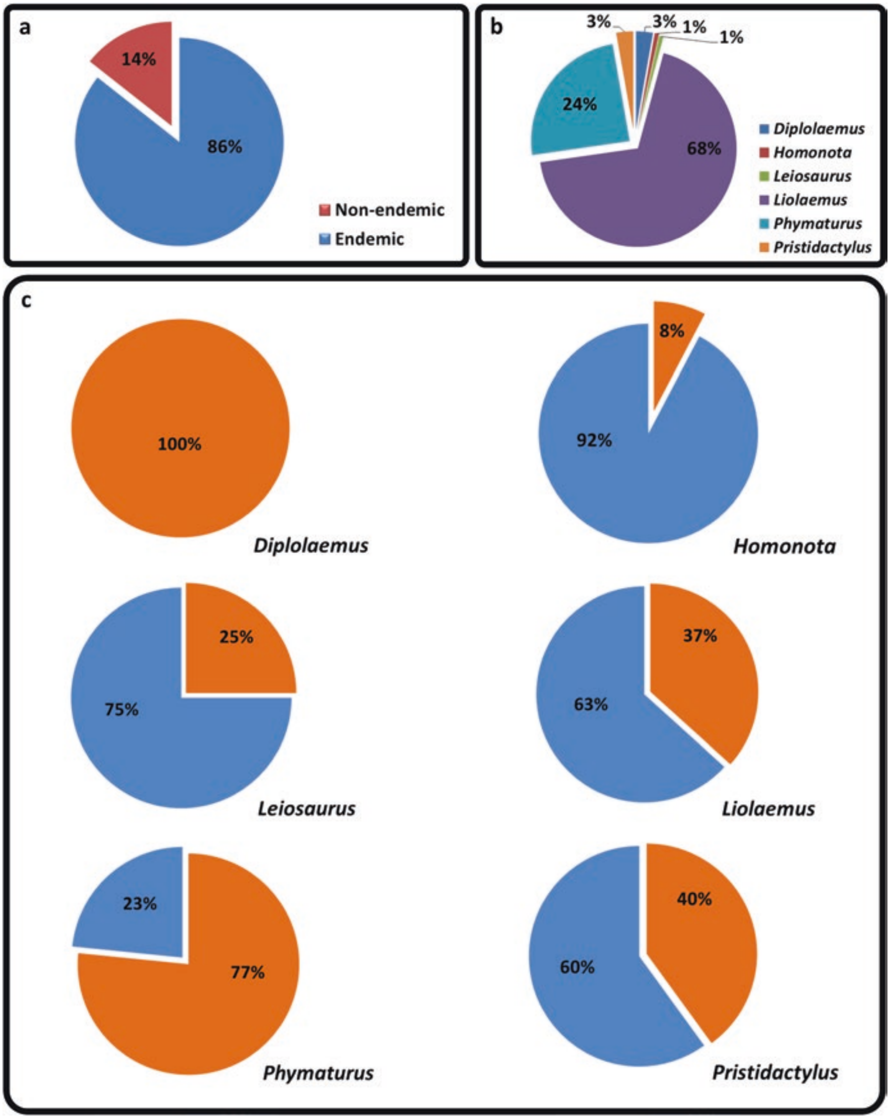

Fig. 7.2 (**a**) Proportion of endemic species in Patagonia (blue), (**b**) Contribution by family to the endemic Patagonian lizard diversity, (**c**) Proportion of endemic species in Patagonia by the eight main genera

recognize species if these are based on specific published studies, as carried out in Lobo et al. (2012b).

7.2 Taxonomy, Species Recognition, and Distribution

We found several distinct features in the Patagonian lizard fauna (Table 7.1), at the familial taxonomic level we can organize the diversity as follows:

- Families with a marginal or uncertain representation in Patagonia: Tropiduridae, Scincidae, and Diploglossidae.
- Families with a low Patagonian diversity but with some species widely distributed in Patagonia: Amphisbaenidae, Teiidae, and Phyllodactylidae.
- Families with a high species richness in Patagonia: Leiosauridae and Liolaemidae.

7.2.1 Families with a Marginal or Uncertain Representation in Patagonia: Tropiduridae, Scincidae, and Diploglossidae

Tropidurids are a large group of neotropical lizards with at least 136 described species. *Stenocercus* is the most speciose genus in this group and one of the most diverse South American lizard genera, with 69 valid taxa (Uetz et al. 2019). This genus is particularly diverse along the Andean Cordillera, from Venezuela in the north to central Argentina in the south (Torres-Carvajal 2007; Teixeira Jr et al. 2016). Teixeira Jr et al. (2016) is the most comprehensive study on lowland species and the most complete revision made for southern South American species of the genus. *Stenocercus pectinatus* is one of the two species distributed solely in Argentina (*S. doellojuradoi* is endemic of Argentinean arid Chaco), and seems to be restricted to dunes and sandy areas of the central region of the country, but extending to the northeastern corner of the Río Negro province (Fig. 7.3). At its southernmost distribution, it seems to be mainly associated with sandy substrate habitats scattered along the lower Colorado River valley. Probably, the southernmost records with vouchered specimens are the citations by Pérez et al. (2011) that correspond to some of the marks in the map (Fig. 4 in Teixeira Jr et al. 2016). Scrocchi et al. (2010) includes some bibliographic records concentrated in the northeastern corner of Patagonia, but they lack voucher references. This species is difficult to find and therefore uncommon in herpetological collections.

One species of skink (Scincidae), *Aspronema dorsivittatum*, has a marginal distribution along the northern boundary of this area, on the eastern slope of the Andes. Despite the presence of a population on the peripheries of San Rafael city, Mendoza Province (Cei 1986, 1993; Cei and Castro 1978; Corbalán and Debandi 2008; our data) (Fig. 7.3), we decided not to include this species in our list. Only a few

Fig. 7.3 Map of the region covered by this study showing the main geographic points cited in the text

specimens of *A. dorsivittatum* have been collected around San Rafael city, and all seem to be restricted to a few hundred meters along the northern branch of the Diamante River on the northern edge of the Diamante Island. Specimens of *Aspronema dorsivittatum* from localities in its southern distribution in Argentina were not found in collections we visited, and all bibliographic citations from Mendoza Province lack vouchered material. Only a single specimen was examined in the LJAMM-CNP IPEEC collection from this region (LJAMM-CNP 17441), collected along the Diamante River (Fig. 7.3). Corbalán and Debandi (2008) do not include any reference material in their study of lizards of Mendoza Province, and apparently repeated bibliographic citations made by previous authors. Gallardo (1968), in a uniquely comprehensive study of Argentinean mabuyas, did not cite any vouchered material from Mendoza Province. Dunn (1935) cited some specimens from northern Mendoza and probably this is the source of some of the dots marked on maps in Cei's monographs (1986, 1993), and in other publications. In the eastern areas of central Argentina, the southernmost record for *Aspronema dorsivittatum* is ~500 km northeast of Río Colorado (Williams and Kacoliris 2011). Confirmation of the presence of this species would add another family (Scincidae) to the lizard fauna of Patagonia, but as it has a marginal distribution and only confirmed at a single site in the northernmost border of our study area, we do not include it here as part of the Patagonian herpetofauna. Habitats potentially suitable for this species exist along the Atuel River basin, but field surveys carried out in these areas, if they exist, have not been published.

Another occasionally cited group of lizards for Patagonia are the South American glass lizards of the family Diploglossidae. Gallardo (1966a) cited *Ophiodes intermedius* for Chubut province (Fig. 7.3), based on the examination of a specimen (MACN 21171) collected apparently by J. Koslowsky. This seems to be the origin of a repeated citation for the presence of this species in Patagonia. Two recent field guides include the species in Patagonia (Scrocchi et al. 2010; Scolaro 2006) but do not mention any vouchered material. Scrocchi et al. (2010) marked a point based on a bibliographic citation in Río Negro Province (Fig. 7.3) but we were unable to find the original source of this record. An unpublished doctoral dissertation by Borges-Martins (1998) is the last comprehensive revision of austral *Ophiodes*; it marked a point for *O. intermedius* in Patagonia based on Gallardo's (1966a) citation. According to Borges-Martins (1998), *O. intermedius* must be restricted to central Argentina and the only species of *Ophiodes* near the Patagonian Phytogeographic Province (hereafter Patagonian Province) is *O. vertebralis*, but all voucher specimens were collected at least 200 km N of Colorado River, the northeastern limit of his study (Fig. 7.3). Williams (1991) mentions the species for some departments (*Partidos*) in southern Buenos Aires province, but without reference to a voucher specimen for that study. Pérez et al. (2011) made a study of herpetofauna of Río Negro province and did not mention any specimen or bibliographic citation for *Ophiodes*, and a comprehensive study on the herpetofauna of Chubut carried out by Minoli et al. (2015), did not cite *Ophiodes* in that province. Koslowsky (1896, 1898) never cited this species for Patagonia, and the origin of the MACN 21171 could be attributed to a Museum collection data-basing error.

7.2.2 Families with a Low Species Diversity but with Some Species Widely Distributed in Patagonia

Two families of lizards that meet this criterion are represented in this area: Phyllodactylidae and Teiidae, as well as the clade Amphisbaenia (Fig. 7.4). Although the latter are not strictly "lizards", we have included them in our review.

Amphisbaenidae is the largest and most geographically widespread amphisbaenian family; it is found in the New World (West Indies and South America) and sub-Saharan Africa (Vidal et al. 2008; Measey and Tolley 2013; Pough et al. 2015). At the time of this work, the genus *Amphisbaena* includes 96 species (Uetz et al. 2019). In South America no amphisbaenids are found on the western side of the Andes, but on the eastern side they are widely distributed in central and eastern temperate regions. Argentinean amphisbaenids have been studied by Montero (1994, 1996, 2016), and two species, both with large distributions north of the Colorado River basin, are present in Patagonia (Fig. 7.4a, b). They are found in low densities in the area included in this book, and represented by only a few scattered vouchers in herpetological collections. *Amphisbaena plumbea* (Fig. 7.4a) seems to be the most common of the two species, it is found along sandy areas of the Monte Phytogeographic Province (hereafter Monte Province; Avila et al. 2007a; Montero 1996; Minoli et al. 2015), including some coastal ecotones along the Atlantic shores reaching Camarones (Chubut) at 45° S (Gans and Diefenbach 1972). In contrast, *A. kingii* (Fig. 7.4b) is known only in few localities on the easternmost part of Monte Province, reaching Golfo Nuevo on the Valdés Peninsula (Daciuk and Miranda 1980; Montero 1996; Minoli et al. 2015). A review of the southernmost records of both species in Chubut province is found in Minoli et al. (2015). Montero (1996) cited a record for *Amphisbaena darwinii* just within the boundaries of our study area, based on a specimen deposited in the San Rafael Municipal Museum in Mendoza. However, this is the only record for this species in the area, and no bibliographic citation or subsequent collections were carried out (to our knowledge) for this species in other localities, making the southern (and Patagonian) distribution suspicious. At this time, the only comprehensive study about the distribution of Patagonian amphisbaenians species is Montero (1996).

Phyllodactylidae is a widespread distributed family with at least 148 described species (Uetz et al. 2019). The family ranges through México, Central and South America, Caribbean islands, northern Africa, Middle East, southern Europe, and some oceanic archipelagos; the Socotra, Canary, Cape Verde, and Galápagos Islands. Although there is strong support for a monophyletic Phyllodactylidae based on molecular data (Gamble et al. 2008), there are so far no morphological synapomorphies to diagnose this family or many of its constituent genera (Daza et al. 2017). In southern South America they are represented only by the genus *Homonota*, with 13 species described from Argentina, Uruguay, Brazil, Paraguay, and Bolivia (Kluge 1964; Morando et al. 2014; Daza et al. 2017; Cacciali et al. 2017, 2018). Diagnosing the genus *Homonota* has been problematic because of its original description and the generic assignment of southern South American geckos has

Fig. 7.4 (**a**) *Amphisbaena plumbea*, Amphisbaenidae, insert: head detail (courtesy of Ignacio Minoli), (**b**) *Amphisbaena kingii*, Amphisbaenidae, insert: head detail, (**c**) *Homonota horrida*, Phyllodactylidae, (**d**) *Homonota underwoodi*, Phyllodactylidae, (**e**) *Homonota darwinii*, Phyllodactylidae, (**f**) *Aurivela longicauda*, Teiidae, (**g**) *Salvator rufescens*, Teiidae (Courtesy Nicolas Pelegrin), (**h**) *Teius oculatus*, Teiidae

been confusing. Early taxonomists placed it in several genera until Kluge (1964) reviewed the taxonomy of *Homonota*. In the following years, the genus *Garthia* was described with the Chilean endemic *G. gaudichaudii* as its type species, but some authors treated it as a synonym of *Homonota* (e.g., Kluge 1991). Recently, molecular phylogenies have confirmed the validity of *Garthia* and rejected the monophyly of a *Homonota* + *Garthia* clade (Gamble et al. 2008, 2011; Morando et al. 2014). *Homonota* geckos are largely terrestrial, found in sandy environments, under leaf litter, rocks, or in pieces of wood (Kluge 1964; Cei 1986, 1993) but *H. horrida* is found on trees in the Chaco. Most species have restricted distributions, but three, *H. horrida* (Fig. 7.4c), *H. underwoodi* (Fig. 7.4d), and *H. darwinii* (Fig. 7.4e), have populations distributed across large ecoregions. These three species reach the area covered by this study, and *H. darwinii* is the only one endemic to Patagonia. *Homonota horrida* is found in the Monte Province and southern Chaco Province, including montane Chaco and some locations in the Wet Chaco. Northern populations seem to be different species and probably *H. horrida* must be restricted only to Argentina (Cacciali et al. 2017, 2018). In Patagonia, *H. horrida* is usually found only on rocky areas of southern Monte Province (Pérez et al. 2008, 2011). *Homonota underwoodi* is usually found only in sandy environments in the Monte Province (Kluge 1964; Cei 1986; Pérez et al. 2005, 2011; Tiranti and Avila 1997), and seems to be restricted to lowland sandy areas. Both species (*H. horrida* and *H. underwoodi*) are found in sympatry in southern Mendoza, eastern Neuquén, and northern Río Negro provinces, and at least in the Añelo basin with *H. darwinii* (Tiranti and Avila 1997; Pérez et al. 2005, 2011; Morando et al. 2014). *Homonota darwinii* is widely distributed across the Patagonian Steppe, and in some habitats of southern Monte Province. *Homonota darwinii* reaches the southernmost distribution of any gecko in the world (Abdala 1998; Piantoni et al. 2006; Aguilar and Cruz 2010; Morando et al. 2014), inhabiting the steppes of Patagonia to at least 51° S in Puerto Deseado, Santa Cruz Province (Fig. 7.3), Argentina, according to Cei (1986).

The lizard family Teiidae includes 160 species allocated to 18 genera, widely distributed across the Americas and West Indies (Uetz et al. 2019), and ecologically characterized as diurnal, terrestrial, or semi-aquatic, and active foragers (Pough et al. 2015). The Teiidae in general have a marginal distribution in northern Patagonia but three genera reach the area covered by this work; all distributed east of the Andes, in the Monte Province: *Aurivela*, *Salvator*, and *Teius*. *Aurivela longicauda* (Fig. 7.4f) is the southernmost distributed teiid lizard; it is found at low densities in the Monte Province habitats and almost reaching the Chubut River, but not crossing it according to our records. *Aurivela* is a new genus proposed by Harvey et al. (2012) to include two species endemic of Monte Province in western Argentina, *A. longicauda* and *A. tergolaevigata*. Despite doubts about the necessity of a division at a generic level for several closely related species (Tucker et al. 2016), the generic name *Aurivela* is still in use. *Aurivela longicauda* was for a long time the only species of teiid lizard exclusive to the Monte Province, but a few years ago, Cabrera (2004) described the northern populations as a new species, *A. tergolaevigata*, using mainly chromatic and morphological characters. This proposal was congruent with an earlier mtDNA phylogeographic study (Yoke et al. 2006). *Aurivela longicauda* is the smallest Patagonian teiid, and has been observed as far south as Punta Flecha, El Doradillo Beach (Fig. 7.3) a few km north of Puerto Madryn city, on the coast of Golfo Nuevo (43° S). It has been collected at similar latitude 200 km west of the coast at Telsen Stream (Frutos et al. 2005). These southern populations are very small and limited to sandy areas along the coast and remnants of sandy areas inland, just south of the Somun Curá plateau. *Salvator rufescens* (Fig. 7.4g) is the largest teiid found in Patagonia, its southernmost populations seem to be restricted to some areas between Negro and Colorado rivers, but an isolated population has been cited for Bajo del Gualicho in eastern Río Negro Province, but without voucher references (Cei and Scolaro 1982; but see Chap. 1, Fig. 1.4d). A photograph purportedly taken at this place is published in Scrocchi et al. (2010). Populations seem to be very small but a survey to confirm the presence of this species in northern Río Negro and eastern Neuquén provinces is still needed. Recent findings/observations of the species in some areas between Negro and Colorado rivers were spread by "social media" in the last 2 years indicating that species distributions and population densities have not been carefully surveyed by herpetologists. Geographic distributions supported by vouchers deposited in recognized collections are reduced (to our knowledge) to a single locality of southwestern La Pampa province, near the Colorado River (LJAMM 11390) (Fig. 7.3). *Teius* is a genus of medium-sized lizards found along the northern boundary of this focal study area (Cacciali et al. 2016). *Teius teyou* is found only in Monte Province habitats along a narrow north-south strip between volcanic outcrops of the northern Payunia region and the western edge of the Atuel River, between San Rafael city and Punta del Agua in Mendoza province. It seems to be a common species in some areas but is strictly limited to these small Monte Province environments. *Teius oculatus* (Fig. 7.4, h) is found in La Pampa and Río Negro provinces (voucher specimens are deposited in LJAMM-CNP collection, see Cacciali et al. 2016), but it appears to be a rare species with small populations confined to a strip of no more than 50 km wide, forming the western-southern margins of the Salado-Chadi Leuvú-Colorado Rivers (Fig. 7.3). No records south of the Negro River were found in our bibliographic searches or in curated collections.

7.2.3 High Biodiversity Families in Patagonia: Leiosauridae and Liolaemidae

Lizards of the families Leiosauridae and Liolaemidae comprise the majority of the lizard fauna in the area covered by this study, with 94% of the species. All Chilean species covered by this chapter belong to these families. A quarter of the species of leiosaurids are exclusive to the Patagonian Province, Cuyan High Andes Province, Valdivian Province forests (the Andean Patagonian Forest), and southern Monte Province, and more than 50% of the described species of liolaemids are endemic of the same region.

7.2.3.1 The Leiosaurids

Leiosauridae includes six genera and 34 described species. Two clades are recognized, one includes the Patagonian species, Leiosaurae (following Schulte et al. 2003; Morando et al. 2015). Several papers addressing higher-level relationships of Squamata based on extensive molecular data (e.g., Wiens et al. 2012; Pyron et al. 2013; Reeder et al. 2015); all support the monophyly of the clade Leiosaurae, and infer Enyaliinae as its sister group. The Enyaliinae includes three mostly semiarboreal or arboreal genera, mainly distributed in central and eastern South America. The Leiosaurae includes three mainly terrestrial genera found in southern South America (Argentina and Chile), with 18 species described. All genera of leiosaurids are found in Patagonia: *Diplolaemus*, *Leiosaurus*, and *Pristidactylus*, with a total of 4, 1, and 4 species, respectively (Fig. 7.5). Morando et al. (2015) presented a molecular-based phylogeny of this clade, and Femenías et al. (2020) completed a phylogeographic study of *Diplolaemus* and *Leiosaurus bellii*, with an updated phylogenetic proposal. Earlier partial revisions based on classical approaches are in Cei et al. (2003) and Victoriano et al. (2010) for *Diplolaemus*, and Cei et al. (2001, 2004) for *Pristidactylus*.

Diplolaemus (Fig. 7.5a–d) lizards are medium-sized and stout diurnal (maximum SVL = 112 mm), oviparous, terrestrial, and insectivorous lizards exclusive to the Patagonian Phytogeographic Province. Almost all of the geographic range of this genus is in Argentina, but a few populations extend into Chile where Patagonian Province steppe habitats are present. *Diplolaemus* is the only lizard genus endemic of Patagonia. Victoriano et al. (2010) published the last revision of this group and solved some of the nomenclatural problems, but *Diplolaemus* is still a complex and understudied clade of lizards, with four described species (Table 7.2).

Four species of *Leiosaurus* have been described, but only one is exclusive to Patagonian Province habitats, *Leiosaurus belli* (Fig. 7.5e). This species has the same general characteristics as *Diplolaemus*, reaching relatively large sizes (maximum SVL = 110 mm) and seems to be exclusive to Monte Province environments or ecotonal areas between Monte and Patagonian Provinces, where it is restricted to lowland areas with sandy soils. All other *Leiosaurus* species occur in northern Monte Province or arid Chaco Province environments.

Pristidactylus is the most diverse genus of Leiosaurae with 10 species, four of which are distributed in Chile, and six in Argentina (Etheridge and Williams 1991; Cei et al. 2001; Avila et al. 2003; Minoli and Avila 2017). They are also large lizards (maximum SVL = 108 mm), oviparous, and mainly insectivorous. Three species occur in the Patagonian environments of Argentina. *Pristidactylus nigroiugulus* (Fig. 7.5f) is found in Patagonian Steppe habitats, *P. fasciatus* (Fig. 7.5g) apparently is typical of flatland sandy habitats of the southern Monte Province, and *P. araucanus* (Fig. 7.5h) seems to be the replacement of *P. nigroiugulus* in steppe environments of northern Neuquén and southern Mendoza provinces. Etheridge and Williams (1991) and Cei et al. (2004) summarized the taxonomic history of this genus. On the western side of the Andes, only one species is found under the coverage of this review, *Pristidactylus torquatus*, a widely distributed species.

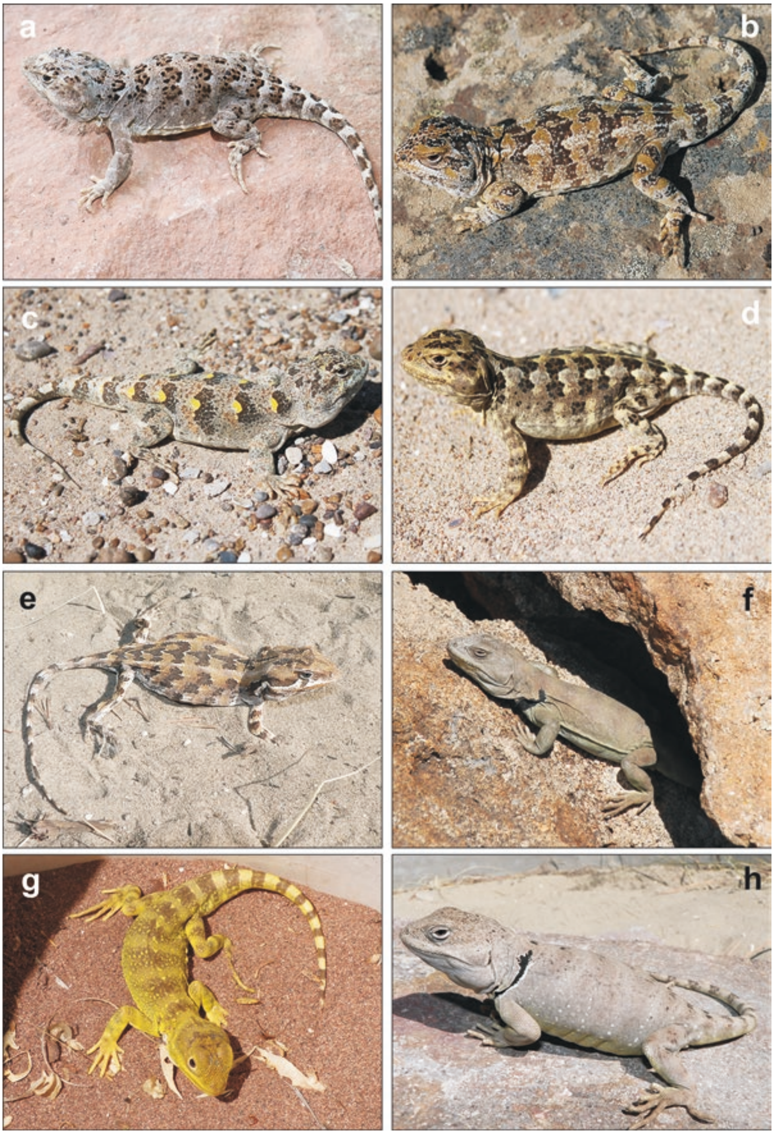

Fig. 7.5 Leiosaurae: (**a**) *Diplolaemus leopardinus*, (**b**) *Diplolaemus darwinii*, (**c**) *Diplolaemus bibronii*, (**d**) *Diplolaemus sexcinctus*, (**e**) *Leiosaurus bellii*, (**f**) *Pristidactylus nigroiugulus*, (**g**) *Pristidactylus fasciatus* (Courtesy M. Victoria Brizio), in our knowledge the first color photograph of an adult male to be published, (**h**) *Pristidactylus araucanus*

7.2.3.2 The Liolaemids

Liolaemidae (or Liolaemini clade for a rank-free category *sensu* Schulte et al. 2003) are small- to medium-sized lizards (but a few reach relatively larger body sizes) and includes three genera, *Ctenoblepharys*, *Liolaemus*, and *Phymaturus*. Originally included in the large family Iguanidae, which was a matter of study and discussion for several decades, the monophyly of the family and each of the three genera is now well established (Townsend et al. 2011; Olave et al. 2019). The number of species in this clade has increased steeply in the last 20 years, climbing from around 150 in early 2000 (Etheridge and Espinoza 2000; Morando et al. 2003) to 265 in mid-2019 (our count). General reviews of the taxonomic and nomenclatural history of this large clade are in Etheridge (1995) and Abdala and Quinteros (2014), as well as in Cei's monographs about Argentinean reptiles (Cei 1986, 1993), Pincheira-Donoso and Núñez (2005), Pincheira-Donoso et al. (2008), but see Lobo et al. (2010b).

Ctenoblepharys
Ctenoblepharys only has one species and is confined to a small coastal area of Perú, but the other two genera are the major components of the Patagonian herpetofauna, and are widely distributed from Perú to Tierra del Fuego across a variety of habitats. The most recent comprehensive revision of this species was made by Etheridge (1995).

Phymaturus
The genus *Phymaturus* comprises lizards with a specialized life history; all species are saxicolous, viviparous, and mostly herbivorous; and all are found on volcanic plateaus of Patagonian and Andean landscapes of Argentina and Chile. Overall, in aspects of their biology, natural history and morphology, they are equivalent to the larger genus *Sauromalus* of North America; both have dorso-ventrally flattened heads and bodies, lateral nuchal skin folds with fat-filled pouches, spiny caudal scales in regular whorls, and several other osteological characters (Etheridge 1995, but see Lobo et al. 2012a, 2015, 2018). First described by Gravenhorst (1838), the genus was poorly studied for more than 150 years, and only one species, *P. palluma*, with two subspecies (*P. p. palluma* and *P. p. patagonicus*) was recognized by Donoso-Barros (1966), and included in the Catalog of South American Squamata by Peters and Donoso-Barros (1970). But the recognized diversity in this genus has changed from a gross underestimate to possibly some overestimation (Becker et al. 2019). The number of species rapidly climbed to almost 50 with the recognition of some of the subspecies of Cei and Castro (1973) and Cei and Roig (1975), as valid species by Etheridge (1995); the revalidation of some previously synonymized species (*P. spurcus* by Lobo and Quinteros 2005a), coupled with an exponential increase in the description of new species after 2000 (e.g., Cei and Videla 2003; Scolaro and Cei 2003; Pincheira-Donoso 2004; Lobo and Quinteros 2005b; Lobo and Abdala 2007; Scolaro and Ibargüengoytía 2007, 2008; Scolaro et al. 2008; Corbalán et al. 2009; Scolaro and Tappari 2009; Scolaro and Pincheira-Donoso 2010; Núñez et al. 2010; Lobo et al. 2010a, 2012c, 2013; Avila et al. 2011, 2014; Troncoso-Palacios and Lobo 2012; Troncoso-Palacios and Esquerré 2014; Lobo and Nenda 2015; González Marín et al. 2016; Troncoso-Palacios et al. 2018b; Hibbard et al. 2019).

However, almost all new species of *Phymaturus* have been described without an explicit species concept or strong methodological (species delimitation) approaches to data collection and analysis, which makes even more difficult to compare species. In some cases, type localities are vague and maps marking localities are completely unintelligible, or authors did not make a detailed comparison among species (highlighted in González Marín 2017). It is not a surprise then, that the same or other authors rapidly sunk (or suggested doing it) some recent descriptions. *Phymaturus agilis*, *P. damasense*, *P. dorsimaculatus*, *P. gynechlomus*, *P. excelsus*, and *P. spectabilis* have been synonymized (or suggested as synonyms) with previously described species (Pincheira-Donoso et al. 2008; Lobo et al. 2010a, 2012b; Becker et al. 2019, Troncoso-Palacios et al. 2018b), and some other species described using a single specimen (e.g., *P. desuetus*) could be of dubious validity. Nevertheless, despite these taxonomic problems, systematic knowledge of this genus grew rapidly during the last 15 years. Espinoza et al. (2004) published the first phylogenetic hypothesis based on mtDNA, soon followed by a morphological study by Lobo and Quinteros (2005a). Since then, several other studies by Lobo et al. (2012a), Morando et al. (2013), Corbalán et al. (2016), Lobo et al. (2015, 2018), González Marín et al. (2018), and Troncoso-Palacios et al. (2018b) have included a variety of molecular and morphological data and analytical methods. Within *Phymaturus*, two groups are recognized (Etheridge 1995): the *palluma* (Fig. 7.6) and the *patagonicus* (Fig. 7.7) groups, whose monophyly was confirmed by several independent studies (e.g., Espinoza et al. 2004; Morando et al. 2013; Pyron et al. 2013). Abdala and Quinteros (2014) made a recent historical review of *Phymaturus* and its nomenclatural and systematic history, as well as Lobo et al. (2015, 2018) for each of the groups. All species of the *patagonicus* group are found in the area covered in this book, as well as half of the described species of the *palluma* group.

Liolaemus

Liolaemus is the most speciose group of lizards of South America. A large number of species are found along the Andes and adjacent arid and semiarid ecoregions in Argentina and Chile, with fewer species in highlands of Perú and Bolivia (although this may be an artifact of limited sampling; Aguilar et al. 2013, 2017, 2019). A small number of species are found along the eastern seaboard of the continent, in the coastal or Mediterranean dunes of Brazil (3), Uruguay (3), and Paraguay (2). Lastly, *Liolaemus chacoensis* is found in the only woody aridland of the world, the arid Chaco (Argentina, Bolivia, and Paraguay), and *L. azarae* on riverine dunes along the Paraná river (Argentina-Paraguay).

Originally included in the large family Iguanidae, an issue of discussion for several decades, the monophyly of Liolaemidae is now well established (Townsend et al. 2011). This clade of iguanians is, without doubt, one of the most interesting and attractive taxonomic groups of New World lizards for research in several fields of biological sciences such as evolution, systematics, biogeography, conservation, physiology, behavior, anatomy, ecology, and general biology (e.g., Breitman et al. 2013; Pincheira-Donoso et al. 2013a, b, 2015; Wollenberg Valero et al. 2019; Olave et al. 2019). Such interest is mainly due to the great diversity of biological and

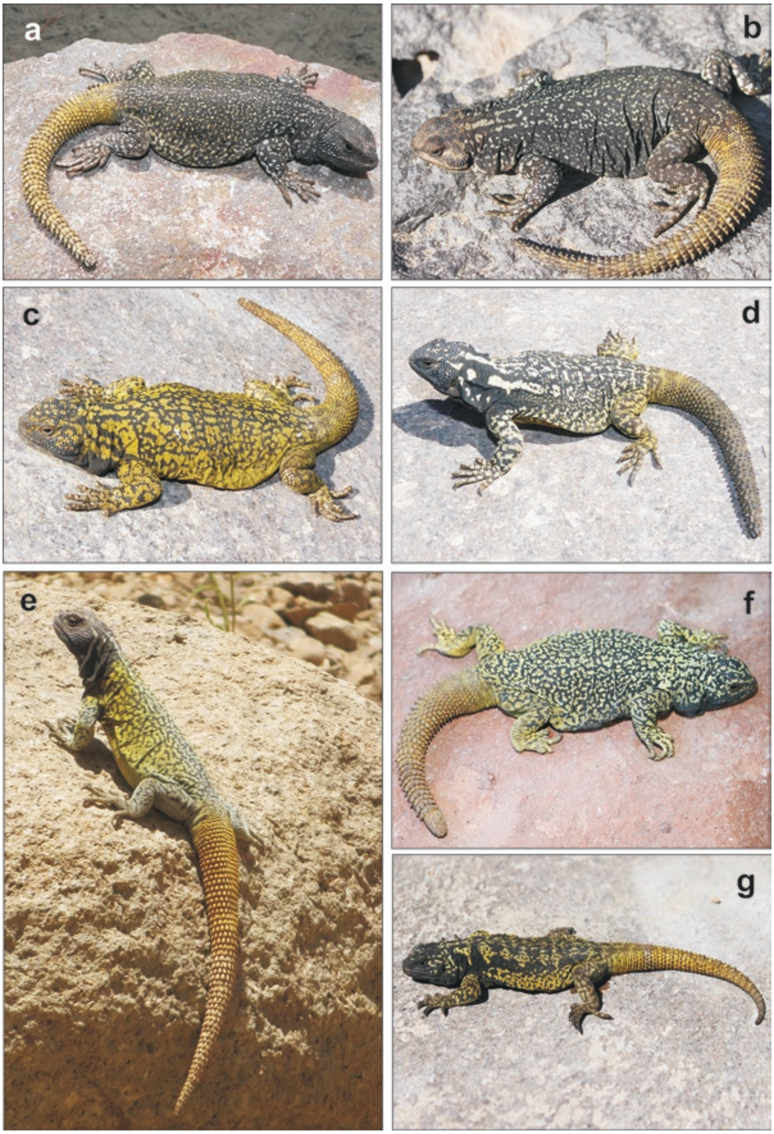

Fig. 7.6 *Phymaturus*, *palluma* group; (**a**) *Phymaturus roigorum*, from the type locality (hereafter TL), (**b**) *Phymaturus tromen* (TL), (**c**) *Phymaturus damasense*, (**d**) *Phymaturus dorsimaculatus* (TL), (**e**) *Phymaturus verdugo*, (**f**) *Phymaturus loboi*, (**g**) *Phymaturus vociferator* (TL)

natural history traits present in this genus, including species with saxicolous, arboricolous, and psammophilous habits, viviparous or oviparous reproductive modes, as well as one parthenogenetic species, and insectivorous, herbivorous, or omnivorous diets. The variety of color patterns (with ontogenetic, sexual, and geographical variation), body sizes, and morphologies makes this genus even more attractive.

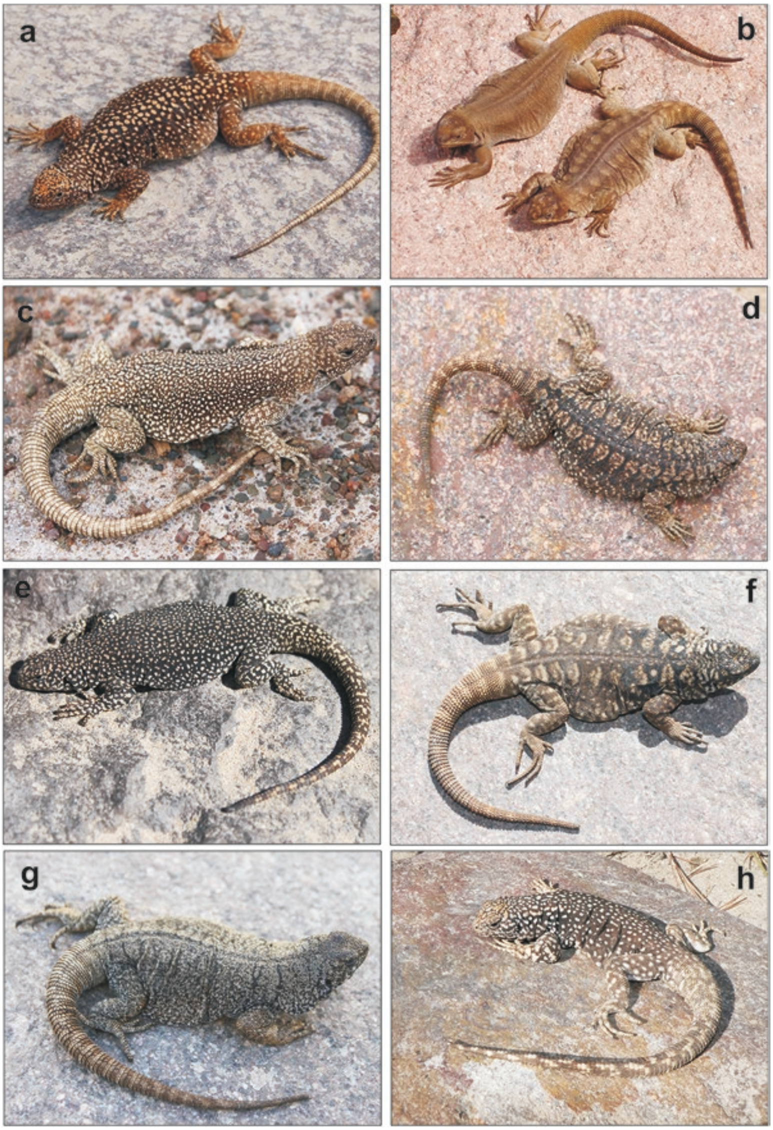

Fig. 7.7 *Phymaturus*, *patagonicus* group: (**a**) *Phymaturus patagonicus* (TL), (**b**) *Phymaturus spurcus* (TL), (**c**) *Phymaturus nevadoi* (TL), (**d**) *Phymaturus felixi* (TL), (**e**) *Phymaturus delheyi* (TL), (**f**) *Phymaturus castillensis* (TL), (**g**) *Phymaturus indistinctus* (TL), (**h**) *Phymaturus yachanana* (TL)

Since the early 1970s several species groups based on morphological similarities were *de facto* accepted by herpetologists. But Raymond Laurent first proposed the recognition of two main groups of *Liolaemus*, *Eulaemus,* and *Liolaemus sensu stricto*, as subgenera or larger groups, in the early 1980s (Laurent 1983, 1985).

Presently, this proposal is well accepted among herpetologists, and species groups based on general appearances have been superseded by groups based on detailed phylogeographic and phylogenetic studies; several well-established groups, complexes, or clades are now recognized by almost all herpetologists. *Eulaemus* is the group with better-established clades, and despite some small taxonomic disagreements, the major clades are strongly supported (e.g., Olave et al. 2014; Morando et al. 2020). The situation is different in the *Liolaemus sensu stricto* clade; some species groups are still understudied and no consensus among herpetologists has been reached (e.g., Panzera et al. 2017). As the scope of this chapter is not to discuss taxonomic, systematic or nomenclatural history, we referred to some key publications for a review of these issues. We avoid citing some problematic publications that advocate for "taxonomic rearrangements" to reduce the spread of "bad taxonomy" ideas; we cite here papers that have made a serious scientific contribution to the knowledge of the family. Further bibliographic references can be found in these papers. Etheridge (1995) summarized some nomenclatural history problems or proposals, and Lobo et al. (2010b) provided a critical review and systematic discussion about some proposed classifications of *Liolaemus*. In 2014, Abdala and Quinteros (2014) reviewed the family Liolaemidae, and later Troncoso-Palacios et al. (2019) presented another proposal to avoid the spread of publications that lacked scientific rigor. Several proposals of group rearrangements have been published (e.g., Lobo 2001, 2005; Avila et al. 2006; Abdala 2007a; Fontanella et al. 2012; Breitman et al. 2013; Olave et al. 2014, 2015; Troncoso-Palacios et al. 2015a); here, we use the arrangement shown in Table 7.3.

Liolaemus Sensu Stricto

Proposed by Laurent (1983) this group includes ~120 species, distributed from the Peruvian highlands to the Patagonian Steppes of Santa Cruz province in Argentina. Only a few species are found in the lowlands east of the Andes, no members of this group are known from Paraguay, Uruguay, or Brazil. The highest diversity is found along the Andes and adjacent mountain ranges, with the majority of the species inhabiting rocky environments. The only known arboricolous species are in this clade, and viviparity likely evolved several times in this group (Schulte et al. 2000; Esquerré et al. 2018). Despite studies focused on a few of the "eastern Andean" groups, relationships among groups within *Liolaemus chiliensis* sensu stricto are uncertain. Recently, Troncoso-Palacios et al. (2015a) proposed the division of the

Table 7.3 Species groups recognized within the Chilean clade (*Liolaemus* sensu stricto) of *Liolaemus* following Troncoso-Palacios et al. (2015a, b) and Panzera et al. (2017)

Subgenus	Section	Group
Liolaemus	*chiliensis*	*alticolor-bibronii*
		chillanensis
		elongatus
		gravenhorstii
		kriegi
		pictus
	nigromaculatus	*monticola*

subgenus into the *L. chiliensis* and *L. nigromaculatus* sections, results confirmed by later studies (Panzera et al. 2017; Esquerré et al. 2018). Panzera et al. (2017) failed to support the monophyly of most species groups previously proposed based on morphological characteristics. One factor that may have influenced this result is that it only included a small number of species. Most *Liolaemus* species in this clade are characterized by unsolved taxonomic or nomenclatural problems, and species boundaries remain a matter of discussion. A well-resolved and strongly supported phylogeny will be needed to clarify the evolutionary relationships in order to establish a straightforward taxonomy. Here, we follow a conservative approach to species grouping.

The *Liolaemus alticolor-bibronii* Group[1]

Lizards in the *L. alticolor-bibronii* group are small and slender (maximum SVL 48–64 mm), oviparous and viviparous, with a "grass-swimmer" lifestyle and body shape. They are usually found in bushy and grassy environments, sometimes with sandy or rocky substrates (Fig. 7.8). Species diversity has expanded quickly since the original recognition of the group (Ortiz 1981; Cei 1986); currently about 30 species (Martínez et al. 2011; Quinteros 2012, 2013; Abdala et al. 2015; Portelli and Quinteros 2018; Vega et al. 2018). The *Liolaemus alticolor-bibronii* clade has the largest latitudinal distribution within the genus, ranging from the Peruvian Andes across the Bolivian Altiplano (Plateau), and south to the Andean Patagonian forest and Patagonian steppes of Argentina and Chile. The clade also inhabits some extra-Andean mountain ranges, including the Sierras Subandinas, Pampeanas, and Tandilia/Ventania systems, as well as lowland regions of the Patagonian and Monte Provinces, and extending to the Atlantic coast of Argentina (Cei 1993; Quinteros 2013; Portelli and Quinteros 2018). Species diversity within the group varies among studies (see Quinteros 2013; Abdala and Quinteros 2014; Portelli and Quinteros 2018 for a more detailed discussion). Quinteros (2013) includes 33 terminal taxa based on morphological data. The relationships resolved by Portelli and Quinteros (2018) are similar to those inferred by Morando et al. (2007) and Martínez (2012). Morando et al. (2007) resolved hidden diversity within the widely distributed species *Liolaemus bibronii* (Fig. 7.8a), part of which was subsequently morphologically confirmed by Quinteros (2013), and later by Portelli and Quinteros (2018). Morando et al. (2007) and Martínez (2012) performed phylogeographic analyses focusing on populations of *L. bibronii* and *L. gracilis* (Fig. 7.8b), and *L. bibronii*, respectively. A number of candidate species were resolved by Morando et al. (2007), one of which was described as *L. cyaneinotatus* (Martínez et al. 2011; Fig. 7.8c).

Cei (1986) proposed the *Liolaemus lemniscatus* group, but listed only the nominal species. Morphological phylogenies confirm the placement of this species in the *L. alticolor* group (later the *L. alticolor-bibronii* group; Lobo 2005; Quinteros 2013), but mtDNA gene trees and combined mtDNA+morphological phylogenies do not affirm the Lobo/Quinteros hypothesis. All mtDNA gene trees infer *L. lemniscatus*

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[1] After closing the search for information for this chapter, four new species from this group were described: *L. balerion*, *L. meraxes* and *L. vhagar* in the Argentine Patagonian steppes, along with a redescription of *L. bibronii* (Quinteros et al. 2019).

Fig. 7.8 *Liolaemus sensu stricto*. (**a**) *Liolaemus bibronii*, (**b**) *Liolaemus gracilis*, (**c**) *Liolaemus cyaneinotatus* (TL), (**d**) *Liolaemus abdalai*, (**e**) *Liolaemus curicencis*, (**f**) *Liolaemus araucaniensis*, (**g**) *Liolaemus chiliensis*, (**h**) *Liolaemus schroederi*

close to the *L. monticola* group, but separated by a deep divergence (Schulte et al. 2000; Troncoso-Palacios et al. 2015a; Torres-Pérez et al. 2017). However, a combined mtDNA + morphology phylogenetic study (Portelli and Quinteros 2018) inferred the *L. lemniscatus* group as sister to the *L. alticolor-bibronii* group, which includes *L. curicensis* (Fig. 7.8e), *L. fuscus*, *L. lemniscatus*, *L. nitidus*, and *L.*

pseudolemniscatus. Portelli and Quinteros (2018) did not present the results of their morphological phylogeny, and probably draw some of their conclusions solely on mitochondrial gene tree. For the moment, we consider *L. lemniscatus* group as a crown taxon not closely related to any other based on the mtDNA gene trees. The Patagonian record of *L. nitidus* is based only on one specimen from Pampa Barrio Norte, Concepción (Troncoso and Ortiz 1987) and needs to be confirmed with additional collections.

The *Liolaemus gravenhorstii* Group

Lizards of the *Liolaemus gravenhorstii* group are small and slender (maximum SVL 65–67 mm), viviparous, mainly insectivorous, and distributed throughout western Patagonia (Portelli and Quinteros 2018). Cei (1986) proposed this group to include *L. gravenhorstii* and *L. cyanogaster*. Lobo (2001) presented a morphological phylogeny expanding this group, to include *L. chiliensis*, *L. nitidus*, *L. robertmertensi*, and *L. schroederi.* Lobo later (2005) updated the morphological phylogeny and found that these species form a single or two separate groups, depending on the type of analysis. Lobo et al. (2010b) based on a conservative interpretation of Lobo (2005) restricted the *L. gravenhorstii* group to *L. cyanogaster*, *L. gravenhorstii*, and *L. schroederi* (Fig. 7.8h); this proposal was recently confirmed in a mtDNA gene tree (Esquerré et al. 2018). On the other hand, the phylogenetic position of *L. chiliensis* is problematic. This is a large *Liolaemus* (maximum SVL 95.3 mm) and one of the few able to vocalize (Labra et al. 2013). While Lobo et al. (2010b) hypothesized that it is closely related to *L. robertmertensi*, this last species seems to be inferred within the *alticolor-bibronii* group in the mtDNA gene tree, and *L. chiliensis* (Fig. 7.8g) does not seem to be related (Morando et al. 2007; Olave et al. 2011). More data on this species are needed, but a recently published mtDNA phylogeny (Esquerré et al. 2018) shows that it is basal to the *L. gravenhorstii* and *L. bellii* groups, this last is composed of Andean *Liolaemus* from central Chile not covered in our study.

The *Liolaemus punmahuida* Group

The *Liolaemus punmahuida* clade is a name used for *Liolaemus punmahuida* (Fig. 7.9a) and *L. flavipiceus* (Fig. 7.9b), and may also include *L. tregenzai* (Medina et al. 2017) (Fig. 7.9c, d). These species are high mountain endemics, still poorly known and with non-conclusive phylogenetic relationships results in the few studies that have included them. They are relatively large (maximum SVL 90–96 mm) and stout species, probably viviparous and omnivorous. These species were originally described as microendemics from isolated and difficult-to-reach high Andean peaks, but in recent years populations closely related to known species (e.g., *L. flavipiceus*) were found in nearby localities in Chile (Garin Aguilar et al. 2013). Further, *Liolaemus thermarum* (Fig. 7.9e), a microendemic in the Baños del Azufre Valley in Mendoza, may also be part of this group based on morphological characteristics, but molecular data were inconclusive about the placement of this species (Medina et al. 2017). The *punmahuida* clade is not recognized by Abdala and Quinteros (2014), but is inferred by Esquerré et al. (2018, 2019).

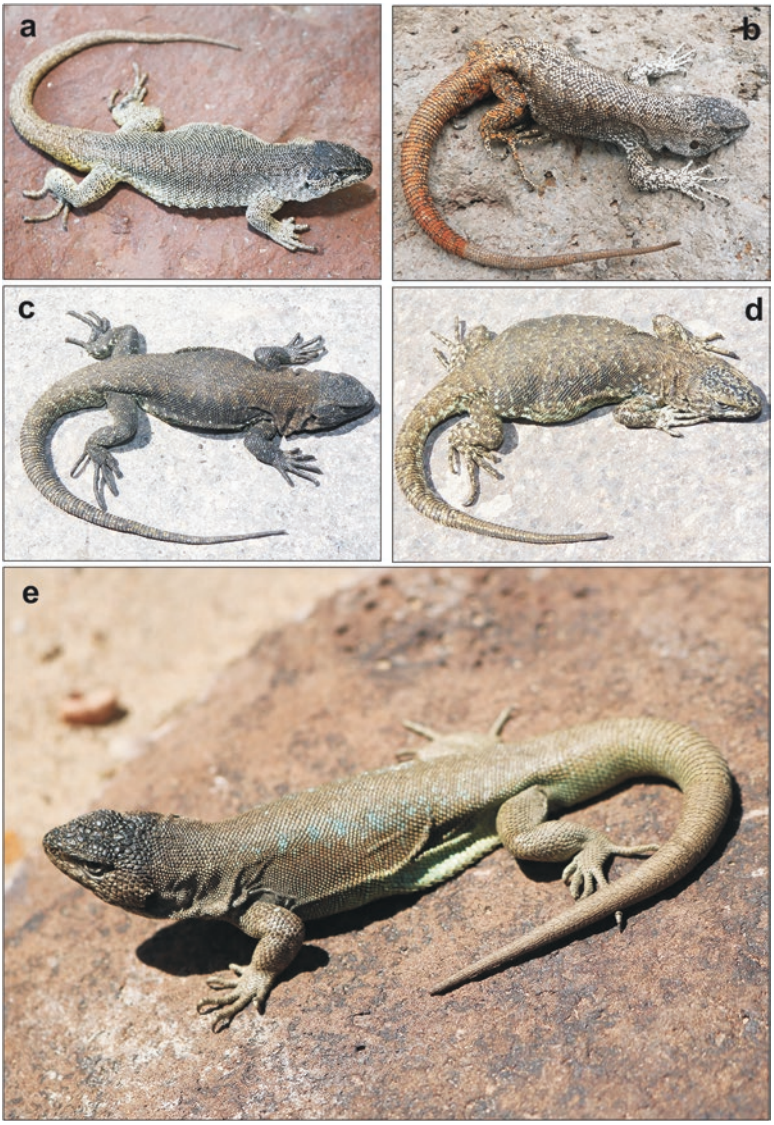

Fig. 7.9 *Liolaemus sensu stricto*. (**a**) *Liolaemus punmahuida* (TL), (**b**) *Liolaemus flavipiceus* (TL), (**c**) *Liolaemus tregenzai* male (TL), (**d**) *Liolaemus tregenzai* female (TL), (**e**) *Liolaemus thermarum* (TL)

The *Liolaemus elongatus-kriegi* Group[2]

The *Liolaemus elongatus-kriegi* group (Fig. 7.10) includes the *L. elongatus*, *L. kriegi*, and *L. petrophilus* complexes (26 described and nine candidate species, following Medina et al. 2017), has been inferred as monophyletic based on several

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[2] After closing the search for information for this chapter, *L. aureum* was described for the northwestern escarpment of the Copahue volcano in Chile (Diaz-Vega et al., 2018).

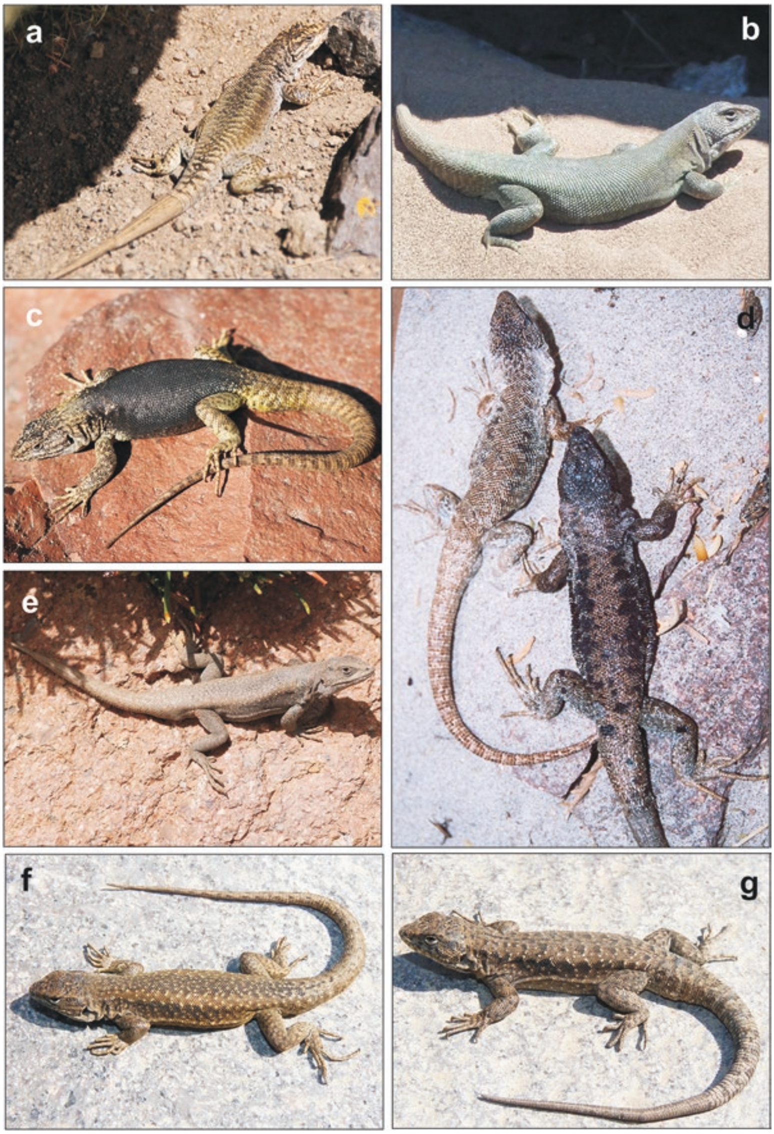

Fig. 7.10 *Liolaemus sensu stricto*. (**a**) *Liolaemus elongatus*, (**b**) *Liolaemus crandalli* (TL), (**c**) *Liolaemus choique* (TL), (**d**) *Liolaemus antumalguen* (TL), (**e**) *Liolaemus smaug* (TL), (**f**) *Liolaemus carlosgarini* (TL), (**g**) *Liolaemus antonietae* (TL)

sources of evidence. Some authors included both the *L. leopardinus* and the *L. punmahuida* clades within this group (e.g., Esquerré et al. 2018, 2019), but this larger clade should receive a different name. Morando et al. (2003) used the name *L. elongatus-kriegi* following the original proposition by Cei (1979; followed by Ortiz 1981), and probably based on some early studies by Cei (1972, 1974a), who also inferred a close relationship between *L. kriegi* and *L. elongatus*. Given the known vs potential Andean distribution of this clade, its diversity and the number of candidate species, additional fieldwork should target remote Andean cordilleras and further phylogeographic and phylogenetic research.

Medina et al. (2017) presented a multilocus phylogeny that is largely congruent with relationships inferred from morphological characters (Lobo 2001; and Lobo et al. 2010b, bibliographical review). These studies inferred the *L. kriegi* complex as sister to the (*L. elongatus* + *L. petrophilus* clades), but Lobo et al. (2010b) also included the *L. punmahuida* clade as part of the *L. elongatus* clade (although these authors had reduced taxonomic sampling). In addition, Esquerré et al. (2014) hypothesized that the *L. leopardinus* clade (*L. leopardinus*, *L. ramonensis*, *L. valdesianus*, *L. ubaghsi*, and *L. frassinettii*) could also be part of the *L. elongatus-kriegi* group, but provided no empirical support for this topology at that time. Recently however, Esquerré et al. (2019) have included the *L. leopardinus* clade as part of the *L. elongatus-kriegi* clade. The *L. elongatus*, *L. petrophilus*, and *L. kriegi* complexes inferred by Medina et al. (2017) are in agreement with results of other authors (Schulte et al. 2000; Lobo 2001, 2005; Lobo et al. 2010b; Pyron et al. 2013), but some authors only recognize two clades, *L. kriegi* and *L. elongatus* groups, with the *L. petrophilus* included in the *L. elongatus* group (Abdala and Quinteros 2014). Partial phylogenies of the group have been included in several species descriptions, but we follow Medina et al. (2017) as the most comprehensive proposal.

The *Liolaemus elongatus* complex: The Argentinean and Chilean diversity of the *Liolaemus elongatus* complex has been underestimated for a long time, and although it has been studied separately for different reasons, there is no unified integrative study. Argentinean diversity was identified as the *L. elongatus* complex, a large set of species/populations distributed from 35° to 45° S (Morando et al. 2003) that includes now seven species: *L. elongatus* (Fig. 7.10a), *L. crandalli* (Fig. 7.10b), *L. choique* (Fig. 7.10c), *L. shitan* (Fig. 7.11a), *L. antumalguen* (Fig. 7.10d), *L. burmeisteri* (Fig. 7.11b), *L. smaug* (Fig. 7.10e), and at least three candidate species: *Liolaemus* sp. 5, *L.* sp. 6, and *L.* sp. 7 (Morando et al. 2003). Some species have been collected only once, e.g., *Liolaemus antumalguen* at the Domuyo Volcano eastern slope (Avila et al. 2010a). Recently, another population of lizards in an area typical of the Monte Province was assigned to this group, *Liolaemus quinterosi* (Ruiz et al. 2019). However, the taxonomy is likely more complex as evidenced by Medina et al. (2017). In this last phylogeographic study (including individuals from the type locality of *L. carlosgarini* (Fig. 7.10f) and a population assigned to *L. chillanensis* from the Argentinean Andes), the authors clearly resolved seven described species (based on a multi-locus data set), but individuals within the *L. elongatus* clade were interdigitated with individuals identified as *L. shitan*. Likewise, the *L. carlosgarini* also included individuals of *Liolaemus* sp. 1, and the *L. antumalguen* haploclade included individuals of *L.* sp. 7 identified by Morando et al. (2003). Medina et al. (2017) also identified three additional candidate species: *L.* sp. 2, *L.* sp. 3, and *L.* sp. 6.

Chilean diversity was neglected until recently, and almost all of the six species that occur in Chile have been only recently described. Núñez and Labra (1985) described *L. curis* from Termas del Flaco, in the O'Higgins region in the Andean highlands. Later, Morando et al. (2003) hypothesized that this taxon could belong to

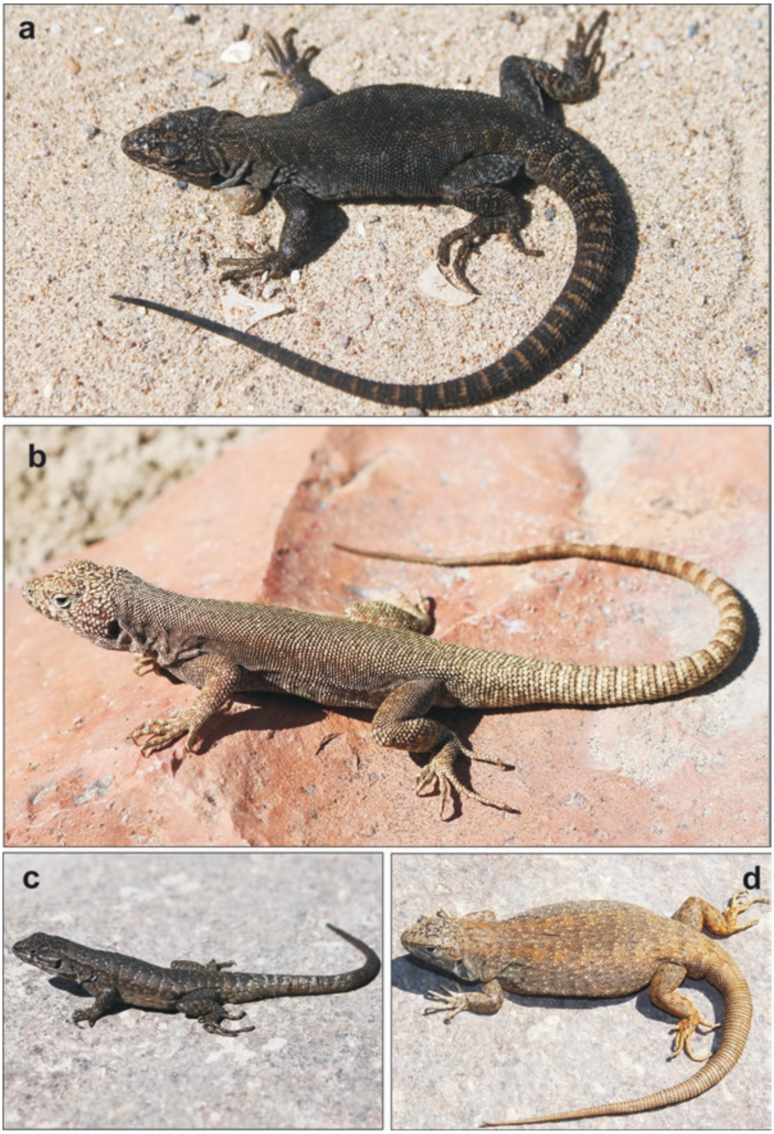

Fig. 7.11 *Liolaemus sensu stricto*. (**a**) *Liolaemus shitan* (TL), (**b**) *Liolaemus burmeisteri* (TL), (**c**) *Liolaemus scorialis* (TL), (**d**) *Liolaemus ceii* (TL)

the *L. elongatus-kriegi* complex, and a phenetic analysis (methodology and character matrix unknown; Pincheira-Donoso and Núñez 2005) placed it in the *L. elongatus* group. Troncoso-Palacios et al. (2018a) published a mtDNA gene tree that also placed *L. curis* within the *L. elongatus* complex. *Liolaemus elongatus* is widely distributed in the Argentinean Patagonia (Minoli et al. 2013), and it was included in the Chilean fauna by Pincheira-Donoso and Núñez (2005) based on specimens in the Pincheira-Donoso personal collection; these authors noted that this species inhabits the Batea Mahuida volcano, in the Araucanía region of Chile. More recently, Escobar Huerta et al. (2015) described *L. lonquimayensis* from Lonquimay volcano, Araucanía region, based on one male and three females, and also included this new species in the *L. elongatus* complex. Troncoso-Palacios et al. (2016a, 2018a), however, based on a mtDNA study that included all type specimens of *L. lonquimayensis*, found that this species cannot be differentiated from *L. elongatus* based on this marker, and proposed that *L. lonquimayensis* is a junior synonym of *L. elongatus.* This study confirms the occurrence of *L. elongatus* in Chile.

Liolaemus carlosgarini was described from Maule Lagoon in the Maule Region of Chile, near the Pehuenche Pass. Esquerré et al. (2013) performed a cladistic analysis of morphological data and inferred a (*L. carlosgarini* + *L. buergeri*) within the *L. kriegi* clade. However, due to the strong morphological similarity with *L. smaug* (in the *L. elongatus* clade and not included in the cladistic analysis), *L. carlosgarini* was hypothesized to belong to the *L. elongatus* complex (Medina et al. 2017). Later, Medina et al. (2018) published a multilocus phylogeny that inferred *L. carlosgarini* as part of the *L. elongatus* clade. More recently, Troncoso-Palacios et al. (2018a, 2019) resolved a mtDNA gene tree showing that *L. carlosgarini* is paraphyletic, with some sequences closely related to *L. smaug* and others to *L. scorialis* (Fig. 7.11c). This result may indicate a possible hybrid origin of *L. carlosgarini* or incomplete lineage sorting. *Liolaemus scorialis* was originally described from the surroundings of Laguna del Laja, and suggested as member of the *L. elongatus-kriegi* complex based on morphology (Troncoso-Palacios et al. 2015b). Later, a mtDNA gene tree placed it as a member of the *L. elongatus* clade, and closely related to *L. carlosgarini* (Troncoso-Palacios et al. 2019). Another new species, *Liolaemus janequeoae*, was recently described from Laguna Verde, in the vicinity of the Tolhuaca Volcano (Troncoso-Palacios et al. 2018a). This species seems to have the most restricted distribution of all Chilean species of the *L. elongatus* complex, but a recent mtDNA phylogeny suggests a close relationship with Argentinian *L.* sp. 3 (Troncoso-Palacios et al. 2019). Finally, *L. antonietae* (Fig. 7.10g) described from Termas de Chillán (also in the Chilean high Andes, Chillán volcano), and formerly referred to as *L. chillanensis* (Torres-Pérez et al. 2009; Escobar Huerta et al. 2015), is the most recent addition of this complex to the Chilean herpetofauna. Clearly, further "targeted" fieldwork is needed in this part of the Andean Cordillera.

Phylogenetic relationships of this species complex are clearly unsolved. The most updated phylogenetic study, based on a multilocus data (nuclear and mtDNA) set (Medina et al. 2018) found three different results, depending on the methodology used. A concatenated Bayesian tree inferred the *petrophilus* and *kriegi* complexes as monophyletic, but the *elongatus* complex as paraphyletic, whereas two different species tree analyses found the *petrophilus* and the the *elongatus* complexes as either monophyletic (SVDquartet) or as paraphyletic (BEAST).

The *Liolaemus petrophilus* complex includes three main clades for which species relationships reflect geographic concordance: the *L. capillitas*, the *L. austromendocinus*, and the *L. petrophilus* clades. The northernmost of these, the

L. capillitas clade (Lobo et al. 2010b), is inferred with strong support by Medina et al. (2018) and includes *L. talampaya*, *L. dicktracy*, *L. tulkas*, *L. umbrifer*, *L. capillitas*, and *L. heliodermis*, as well as several still undescribed species, but it is not distributed in the area covered by this book. Three species with relatively central distributions between the northern and the southernmost taxa within this complex (*L. austromendocinus*—Fig. 7.12a, *L. gununakuna*—Fig. 7.12b, *L. parvus*) are part of the *L. austromendocinus* clade, but only the two first species inhabit Patagonia. Medina et al. (2018) resolved two well-supported independent lineages within the *L. petrophilus* complex, but only the nominal species (Fig. 7.12c) is recognized as valid, and no further studies have been initiated.

The *Liolaemus kriegi* complex: This group includes four described (*L. kriegi*, *L. ceii*, *L. buergeri*, *L. zabalai*), and two candidate species (*L.* sp. C, *L.* sp. D). The *L. kriegi* clade is represented in the western slope of the Andes by two species: *L. buergeri* (Fig. 7.12d), distributed in Chile from its type locality in El Planchón to Laguna del Maule, both in the Maule region (Troncoso-Palacios et al. 2015a), and in northwestern Neuquén province, Argentina (Medina et al. 2014). On the other hand, the Chilean population of *L. kriegi*, recorded by Donoso-Barros (1974), but also widely known as candidate species *L.* sp. A (Morando et al. 2003; Medina et al. 2014), was described as *L. zabalai* by Troncoso-Palacios et al. (2015a). This species is mainly distributed in northwestern Neuquén province (Medina et al. 2014), while in Chile it only occurs in the surroundings of the Laguna del Laja, Pichachén pass (Troncoso-Palacios et al. 2015a). The species of the *L. kriegi* clade have been compared through morphological analysis, including intersexual variation (Medina et al. 2013), and also via multilocus phylogenetic analyses (Medina et al. 2014, 2015). Samples of *Liolaemus ceii* (Fig. 7.11d) were always found intermixed with samples of *L. kriegi* (Fig. 7.12e) in several studies (Morando et al. 2003; Medina et al. 2015), but a further integrative study of these populations/species is needed in order to test these species boundaries.

The *Liolaemus pictus* Group

The *Liolaemus pictus* group comprises species with varied habitat use, arboreal in some areas, saxicolous in others; all species are viviparous (Pincheira-Donoso and Núñez 2005), and medium sized (maximum SVL 55–72 mm). *Liolaemus pictus* formerly included several subspecies, a proposal now not supported. Cei (1986) proposed the *L. pictus* group listing *L. p. pictus* and *L. p. argentinus*. Lobo (2001) performed phylogenetic analyses (morphological, karyotype, and ecological data) and found that the *L. pictus* group included *L. p. pictus*, *L. p. talcanensis*, and elevated *L. argentinus* and *L. chiloensis* to full species. Lobo (2005) updated phylogenies included the same species but stated that *L. brattstroemi* (previously described as subspecies of *L. cyanogaster*), *L. coeruleus*, and *L. neuquensis* should be included in the *L. pictus* group. Pincheira-Donoso and Núñez (2005) performed a phenetic analysis (methodology and character matrix unknown) and listed in the *L. pictus* group two species: *L. brattstroemi* and *L. pictus*; the latter including six subspecies: *L. p. argentinus*, *L. p. chiloensis*, *L. p. codoceae*, *L. p. pictus*, *L. p. septentrionalis*, and *L. p. talcanensis*. Lobo et al. (2010b), based on Lobo (2005), proposed an

Fig. 7.12 (**a**) *Liolaemus austromendocinus*, (**b**) *Liolaemus gununakuna*, (**c**) *Liolaemus petrophilus*, (**d**) *Liolaemus buergeri* (TL), (**e**) *Liolaemus kriegi*, (**f**) *Liolaemus pictus*, (**g**) *Liolaemus septentrionalis*

arrangement of the *L. pictus* group that included all taxa listed by Pincheira-Donoso and Núñez (2005), and added *L. coeruleus* and *L. neuquensis*. *Liolaemus brattstroemi* is also a problematic taxon in that while the type locality is well defined, the only known specimens are the two female types (not located *fide* Frost and Etheridge 2016), two specimens (MZUC 165139–40; Universidad de Concepción; Lobo

2005), four specimens of Pincheira-Donoso personal collection, and one in the British Museum of Natural History (BMNH-69.5.3.45.46; Pincheira-Donoso and Núñez 2005). Presently, no molecular phylogenetic study on the *L. pictus* group has been carried out, but two *L. pictus* phylogeographic studies are available. Vidal et al. (2012) found no support for most of the subspecies of *L. pictus* (*L. p. argentinus*, *L. p. chiloensis*, *L. p. codoceae*, and *L. p. talcanensis*). This result agrees with the Vera-Escalona et al. (2012) phylogeographic study of *L. p. argentinus*, *L. p. chiloensis*, *L. p. pictus*, and *L. p. septentrionalis*. This study included the mitochondrial cyt-b gene and two nuclear loci, and found no support for any of the above subspecies except *L. p. septentrionalis*. Vera-Escalona et al. (2012) suggested recognition of this taxon as a full species. Troncoso-Palacios et al. (2018a) mtDNA gene tree suggests that *L. pictus* (Fig. 7.12f) and *L. septentrionalis* (Fig. 7.12g) are not sister species, and that *L. neuquensis* is closely related to *L. coeruleus* (Scolaro et al. 2007), and not part of the *L. pictus* group. Here, we follow Troncoso-Palacios et al. (2018a) and exclude these species from this group.

Another mtDNA study (Troncoso-Palacios et al. 2015a) indicated that *L. araucaniensis* belongs to the *L. pictus* group, in agreement with morphological similarities between *L. araucaniensis* (Fig. 7.8f) and juvenile specimens of *L. pictus* (Troncoso-Palacios, unpublished data). In contrast, *L. araucaniensis* is included within the *L. alticolor-bibronii* group by Abdala and Quinteros (2014), but as the outgroup of the *L. alticolor-bibronii* clade by Quinteros (2013), and Portelli and Quinteros (2018). In summary, the *L. pictus* group is currently composed of four species: *L. araucaniensis*, *L. brattstroemi* *L. septentrionalis* and *L. pictus*, but a more comprehensive multilocus phylogenetic/phylogeographic study on this group is needed to resolve the taxonomic issues described here.

The *Liolaemus tenuis* Group

The taxonomic relationships of *Liolaemus tenuis* (Fig. 7.12a) have been fluid. Müller and Hellmich (1933) described a subspecies *L. t. punctatissimus*, then Cei (1986) proposed that the *L. tenuis* group included the two subspecies plus *L. coeruleus*. Lobo's (2001, 2005) morphological phylogenies suggested the addition of *L. neuquensis*, and later suggested these as sister groups in Lobo (2005). Torres-Pérez et al. (2009) found that *L. tenuis* is related to the pair *L. monticola* and *L. nitidus* (Fig. 7.13c), Lobo et al. (2010b) merged the *L. tenuis* group with the *L. pictus* group; but the most recent studies inferred *L. tenuis* as the sister species of *L. pseudolemniscatus* (Troncoso-Palacios et al. 2016a; Torres-Pérez et al. 2017), and that they are not closely related to other *Liolaemus*. Vidal et al. (2004) allozyme study (nuclear genes) found no support for the recognition of two subspecies in *L. tenuis*. Panzera et al. (2017), however, found that *L. tenuis* appears to be composed by more of one taxon, but its phylogenetic position remained difficult to place, probably because they used a limited data set.

The *Liolaemus chillanensis* Group

The *Liolaemus chillanensis* group is composed of three species. Lobo's (2001) early phylogenetic study mainly based on meristic and color features, found *L. chillanensis* (Fig. 7.13b) as part of the *L. monticola* group, but in a later morphological

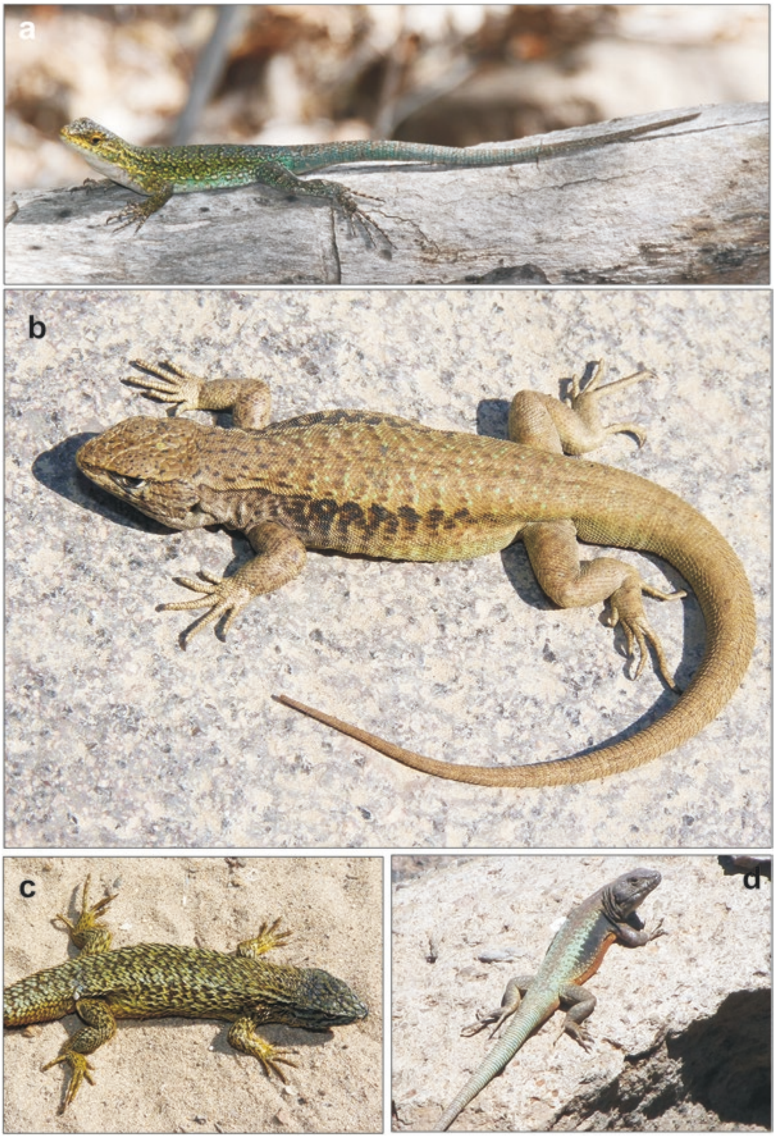

Fig. 7.13 *Liolaemus sensu stricto*. (**a**) *Liolaemus tenuis,* (**b**) *Liolaemus chillanensis* (TL), (**c**) *Liolaemus nitidus*, (**d**) *Liolaemus cristiani* (TL, JTP Photo)

phylogeny (Lobo 2005) found *L. chillanensis* and *L. villaricensis* as sister species, forming a clade outside the *L. monticola* group. Pincheira-Donoso and Núñez (2005) based on a phenetic analysis included both *L. chillanensis* and *L. villaricensis*, as subspecies of *L. chillanensis*; however, these authors did not describe their methodology, their results are not replicable (Lobo et al. 2010b). Lobo et al. (2010b) listed both at the species level and named this clade as *Liolaemus chillanensis* group. A major problem, however, is that the name "*L. chillanensis*" has been used to refer to two unrelated *Liolaemus* that occur sympatrically in Termas de Chillán, and the identity of the true *L. chillanensis* has only recently been clarified (Troncoso-Palacios et al. 2018a). According to Troncoso-Palacios et al. (2018a), *L. villaricensis* does not form part of the *L. chillanensis* group; it includes *L. chillanensis* and *L. cristiani*, this last species described from Maule region. *Liolaemus chillanensis* and *L. cristiani* share bluish coloration and lack precloacal pores (Troncoso-Palacios et al. 2018a), but their life history traits are almost unknown. Further, the record of *L. cristiani* in the Araucanía region (Escobar-Huerta and Ortiz 2011) is almost surely a misidentification, this specimen probably corresponds to the recently described *L. leftrarui*. Finally, Esquerré et al. (2013) described *L. riodamas* based on one population previously attributed to *L. kriegi* by Núñez and Torres-Mura (1992). They performed a cladistic analysis on a morphological data set and inferred *L. riodamas* as the sister species of *L. cristiani*. Although this result should be taken with caution, since only nine *Liolaemus* species were included in the analysis, for the moment *L. riodamas* should be considered as part of the *L. chillanensis* group due to its close relationship with *L. cristiani*. *Liolaemus villaricensis* has historically been interpreted as related to both *L. monticola* and *L. chillanensis* groups, but DNA phylogenetic studies (Torres-Pérez et al. 2009; Troncoso-Palacios et al. 2016a, 2018a) suggest that this species is not related to either of these groups. Moreover, Troncoso-Palacios et al. (2016a, 2018a) found that *L. villaricensis* forms a still unnamed clade with *L. leftrarui*; these species are distributed in the region of the Villarrica and Tolhuaca volcanoes, respectively.

The *Liolaemus monticola* Group

The *Liolaemus monticola* group is composed of four species, all confined to volcanos and mountain ranges of the western Andean slope in Chile. It has a confusing and problematic taxonomic history. Müller and Hellmich (1932) described three subspecies and made reference to a fourth candidate subspecies within *L. monticola*: *L. m. monticola*, *L. m. chillanensis*, *L. m. villaricensis*, and *L. m.* ssp.; this latter never clearly identified. Later, Lobo (2001) performed a phylogenetic study based on morphological (mainly meristic and color pattern data), karyotype, and ecological data, and proposed recognition of a three species *L. monticola* group: *L. chillanensis*, *L. monticola* and *L. villaricensis*. Lobo (2005) updated his phylogeny adding more morphological characters, and recognized that these species are not closely related. Lobo et al. (2010b), based on Lobo (2005), provided a new arrangement for the *L. monticola* group: *L. monticola* and *L. confusus*, this latter inferred as closely related to *L. monticola* in its description (Núñez and Pincheira-Donoso 2006). MtDNA gene trees did not infer this group in its original composition; *L. chillanensis* and *L. villaricensis* are neither related to *L. monticola* nor to each other (Torres-Pérez et al. 2009; Troncoso-Palacios et al. 2018a). Moreover, other similar mtDNA studies expanded the composition of the *L. monticola* group (Troncoso-Palacios et al. 2015a, 2016a; Torres-Pérez et al. 2017) to include: *L. monticola*, *L. confusus*, *L. nitidus*, *L. curicensis*, and one candidate species known as "*L. monticola* southern race" (Lamborot 1991). The record of *L. monticola* in the Patagonian region corresponds to the "*L. monticola* southern race", whose distribution extends to Los Queñes, Maule (Lamborot 2001). Introgression has been detected between "*L. monticola* southern race" and *L. nitidus*, but not between "*L. monticola* southern race" and *L. monticola* (Torres-Pérez et al. 2017) that have allopatric distributions. Remarkably, *L. monticola* and "*L. monticola* southern race" are not sister lineages, as *L. monticola* was inferred as the sister species of *L. nitidus* (Torres-Pérez et al. 2009, 2017); although *L. monticola* and "*L. monticola* southern race" cannot be differentiated morphologically while *L. nitidus* is easily distinguishable from both. This may represent still incomplete knowledge or an extraordinary case of parallel evolution in *Liolaemus* that should be more deeply studied. Finally, *L. confusus* has a very restricted distribution; it appears confined to an area estimated at 11 km^2 (Ramírez-Álvarez et al. 2016).

***Eulaemus* Subgenus**

This is the largest of the two recognized clades of *Liolaemus* in species numbers, including ~156 species. It is distributed in Argentina, Bolivia, Brazil, Chile, Perú, Paraguay, and Uruguay, but the majority of the species of the genus are found in the eastern Andean lowlands, and the Patagonian and Puna aridlands. Multiple studies have consistently inferred two large clades within *Eulaemus*, the *L. lineomaculatus* and *L. montanus* sections (Schulte et al. 2000; Morando et al. 2004, 2020; Avila et al. 2006; Abdala 2007a, b; Fontanella et al. 2012; Olave et al. 2014, 2015), with several groups or complexes within each. Here we use the arrangement shown in Table 7.4.

The *Liolaemus lineomaculatus* Section

The *Liolaemus lineomaculatus* section currently includes 22 species; this is a clade of small- to large-sized lizards (maximum SVL 59–101 mm), usually with a stout body, general dark coloration but with bright lines, spots or bands of yellow, blue, orange, or red colors. They are viviparous, insectivorous, with little sexual dimorphism, and highly variable in coloration and color patterns. They are inhabitants of the Patagonian steppe environments, from highlands of southern Neuquén to the southern tip of the continent and the north of Tierra del Fuego Island. This clade includes the southernmost species of the genus *Liolaemus* and the southernmost lizard in the world, *Liolaemus magellanicus* (Breitman et al. 2013 for an historical review). Almost half of the species described in this group were based on studies carried out by only two authors, J.M. Cei and J.A. Scolaro (Breitman et al. 2013). The name of this section was proposed in a phylogenetic study of *Liolaemus* for the clade composed of *L. lineomaculatus*, *L. somuncurae*, and *L. magellanicus* (Schulte et al. 2000), its monophyly was later supported in other studies that included more species of this group (e.g., Breitman et al. 2011a; Olave et al. 2014). The last described species for the section was *L. yatel* (Abdala et al. 2014), considered as part of the *L. lineomaculatus* group or maybe an intermediate lineage between this and the *L. magellanicus* group according to Abdala et al. (2014). Phylogeographic and morphological studies of Breitman et al. (2011a, b, 2012, 2013, 2015a, b) identified at least six candidate species within the *L. kingii* group (clades 1 and 2 in

Table 7.4 List of main recognized groups within the *Eulaemus* subgenus, following Etheridge (1993, 1995), Schulte et al. (2000), Avila et al. (2006), Abdala (2007a, b), Lobo et al. (2010a, b, c), Fontanella et al. (2012), and Breitman et al. (2011a, b, c, 2012, 2013) (*melanops* series = *goestchi* group + *telsen* group, Abdala 2007a; = *melanops* group, Abdala and Quinteros 2014)

Subgenus	Section	Series	Group/complex
Eulaemus	*lineomaculatus*		
			lineomaculatus
			magellanicus
			kingii
	montanus	*nigriceps*	*darwinii*
			montanus
		melanops	*anomalus* *wiegmannii* *boulengeri*
			rothi
			donosobarrosi
			fitzingerii

Breitman et al. 2015a, *L.* sp. A, *L.* sp. 4, *L.* sp. 5, and *L.* sp. 8 in Breitman et al. 2013, Breitman et al. 2015b), and five within the *L. lineomaculatus* group (lineages 3, 4, 6, 8, and 9 in Breitman et al. 2012 ; Breitman et al. 2011a; Chap. 9). According to Breitman et al. (2013) there could be at least 11 candidate species within the *L. lineomaculatus* section; all need in-depth studies to confirm or reject their specific status. A proposal well supported by morphological and molecular data recognized three main clades (Breitman et al. 2013: the *L. lineomaculatus*, *L. magellanicus*, and *L. kingii* clades.

The *L. lineomaculatus* group includes seven species: *L. avilae*, *L. hatcheri*, *L. kolengh*, *L. lineomaculatus*, *L. morandae*, *L. silvanae*, and *L. yatel* (Fig. 7.14). The distribution of these species extends from central Neuquén (Cei 1986; Christie 2002) along the mountains of western Chubut to south of Santa Cruz province to the shores of the Magellan Strait, with some species more widely distributed and others geographically restricted. The clade and the morphological characters that define it were established by Etheridge (1995), an absence of precloacal pores and presence of dorsal tridentate (or trifid) scales. This group was inferred as monophyletic with mitochondrial (Espinoza et al. 2004; Schulte II and Moreno-Roark 2010) and nuclear genes, these latest study using concatenation as well as a species tree approach (Breitman et al. 2011a).

The *L. magellanicus* group includes *L. magellanicus* and *L. caparensis*; these have the southernmost distributions of the *L. lineomaculatus* section and the entire genus. *Liolaemus caparensis* is only known from its type locality (Breitman et al. 2011c), whereas *L. magellanicus* is widespread south of the Santa Cruz river and is the only species of *Liolaemus* inhabiting Tierra del Fuego Island (Bottari 1975; Jaksić and Schwenk 1983). The *L. magellanicus* group is a well-differentiated clade in both molecular and morphological characters from the other groups of the *L. lineomaculatus* section.

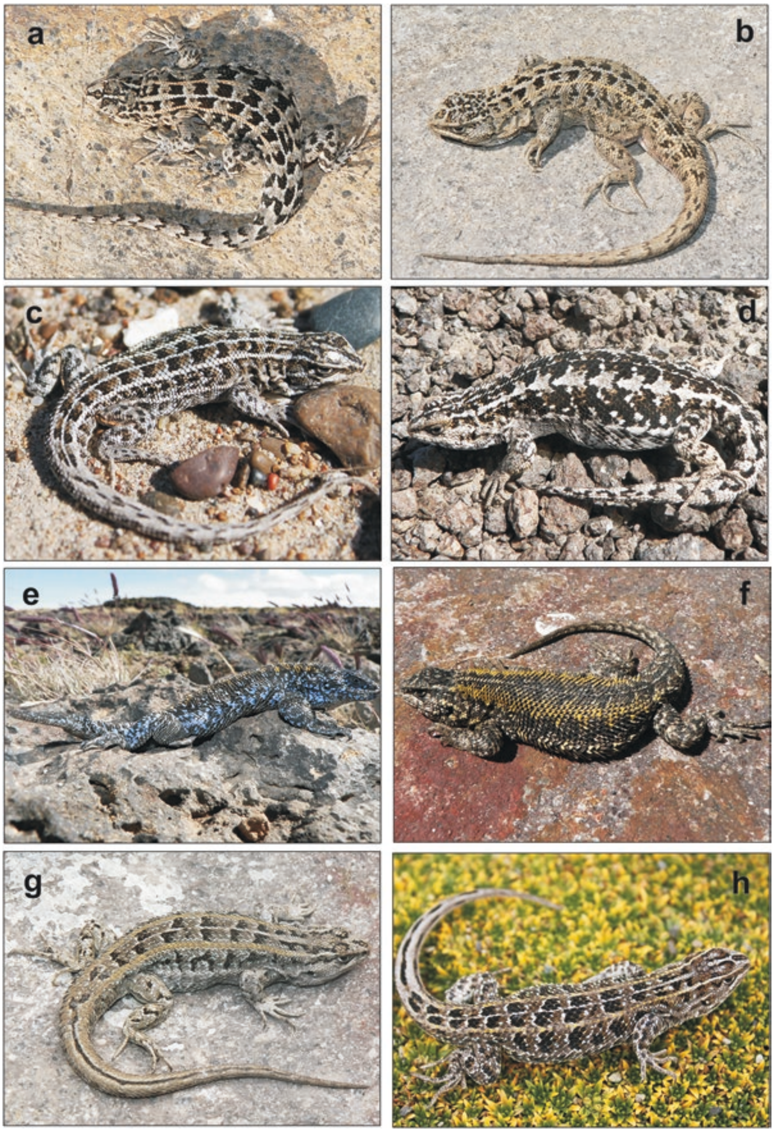

Fig. 7.14 *Eulaemus*. (**a**) *Liolaemus avilae* (TL), (**b**) *Liolaemus lineomaculatus*, (**c**) *Liolaemus morandae* (TL), (**d**) *Liolaemus hatcheri* (TL), (**e**) *Liolaemus sylvanae* (TL), (**f**) *Liolaemus kolengh* (TL), (**g**) *Liolaemus caparensis* (TL), (**h**) *Liolaemus magellanicus*

Breitman et al. (2013) set up a "new" starting point for the species of the previously known as *L. archeforus-kingii* group (e.g., Abdala and Quinteros 2014) because the traditional differentiation into two groups (*L. kingii* and *L. archeforus*), was not supported either by molecular or morphological data (Espinoza et al. 2004; Schulte II and Moreno-Roark 2010; Breitman et al. 2011a, c), thus they

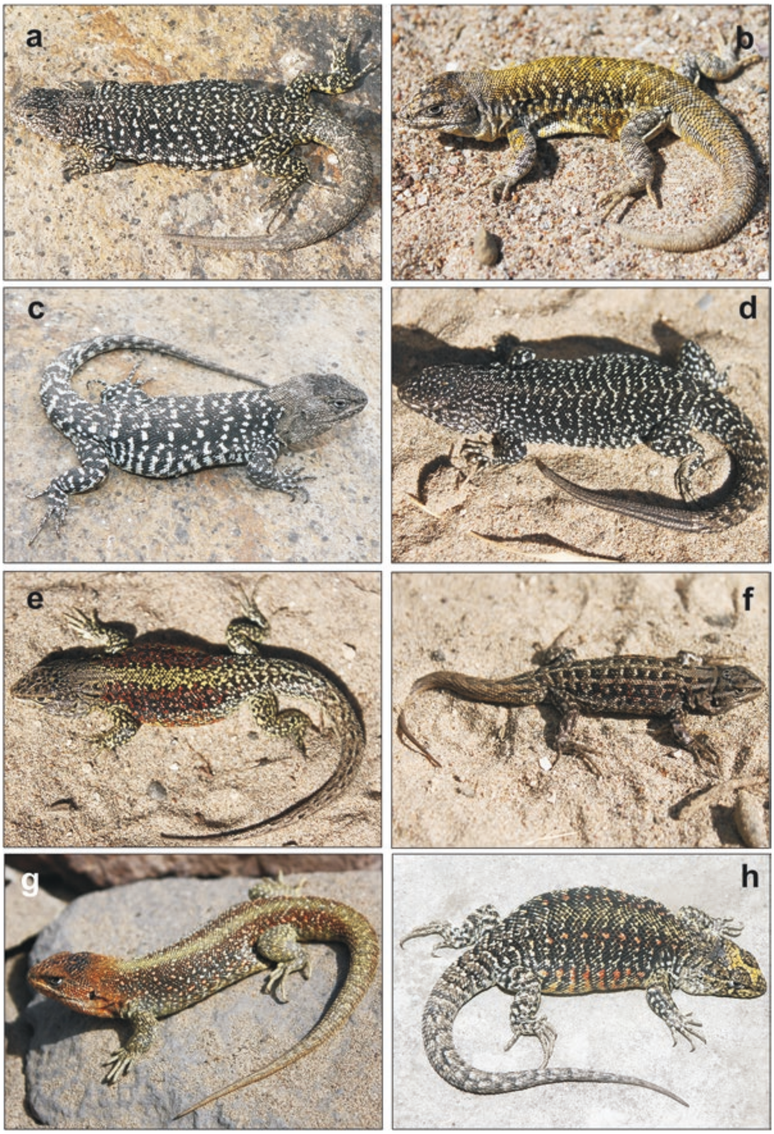

Fig. 7.15 *Eulaemus*. (**a**) *Liolaemus archeforus* (TL), (**b**) *Liolaemus kingii*, (**c**) *Liolaemus baguali* (TL), (**d**) *Liolaemus chacabucoense*, (**e**) *Liolaemus zullyae* (TL), (**f**) *Liolaemus scolaroi*, (**g**) *Liolaemus uptoni* (TL), (**h**) *Liolaemus escarchadosi* (TL)

recommended the name *L. kingii* to refer to the clade formed by: *L. archeforus*, *L. baguali*, *L. chacabucoense*, *L. escarchadosi*, *L. gallardoi*, *L. kingii*, *L. sarmientoi*, *L. scolaroi*, *L. somuncurae*, *L. tari*, *L. tristis*, *L. uptoni*, and *L. zullyae* (Fig. 7.15). Nested within this clade is the strongly supported *L. somuncurae* clade, which includes *L. somuncurensis* and *L. uptoni*. In contrast to the *L. magellanicus* group, some of these species have relatively large distributions (e.g., *L. escarchadosi*, *L. gallardoi*, *L. kingii*, and *L. sarmientoi*), whereas others are more restricted (e.g., *L. somuncurae*, *L. tari*, *L. tristis*, and *L. uptoni*). The *L. kingii* group is well differentiated from the *L. lineomaculatus* and *L. magellanicus* groups based on molecular and morphological evidence, as described by Breitman et al. (2013). As in other *Liolaemus* groups, some problems still exist with some of these species. Descriptions of some species were made decades ago, and sometimes based on unclear diagnostic characters, some type specimens are poorly preserved, and almost all species' type localities are obscure, poorly described and referenced, and difficult to find. The majority of species descriptions are based on very few individuals that do not account for the extensive sexual and ontogenetic polymorphism present in the clade. Further, in the case of *L. kingii*, the use of molecular data has only added uncertainties (Breitman et al. 2013, 2015a, b).

Studies of lizards of the *L. lineomaculatus* section have three well marked time periods: (1) early discoveries in the nineteenth century, (2) a second wave in the last quarter of the twentieth century with the description of several new species and some statistically based morphological studies, and (3) a last period that began with the first phylogenetic and biogeographic analysis employing molecular characters (allozymes) and a cladistic analysis that included species of the *L. lineomaculatus* section (Young-Downey 1998). These studies now continue with access to previously unexplored places, coupled with the use of molecular data that allow the identification of "candidate species" (Breitman et al. 2013), and a more thorough description of new species. Several studies not focused on this section have confirmed its monophyly using different classes of data (e.g., Schulte et al. 2000; Lobo 2001; Lobo and Abdala 2002; Morando 2004; Espinoza et al. 2004; Schulte II and Moreno-Roark 2010). Breitman et al. (2011a), using nuclear and mitochondrial markers and two phylogenetic approaches (species tree and concatenation with Bayesian Inference, Maximum Likelihood, and Maximum Parsimony), presented the first molecular phylogeny for this group. Breitman et al. (2013) is the last comprehensive study of this section of *Eulaemus*.

The *Liolaemus montanus* Section

The most species-rich group within *Eulaemus* is the *L. montanus* section. However, at more recent levels of divergence, there is discordance between hypotheses of phylogenetic relationships between the main clades within the *L. montanus* section from studies using morphological, molecular, or different data combinations (Avila et al. 2006; Abdala 2007a; Abdala et al. 2012a, b; Fontanella et al. 2012; Olave et al. 2014; see all proposed alternative hypotheses in Olave et al. 2015 and Chap. 9 for further details). Fontanella et al. (2012) based on two mitochondrial and two nuclear markers proposed two series within the *L. montanus* section: 1—The *L. nigriceps* series, including the *L. anomalus*, *L. darwinii*, *L. montanus*, and *L. wiegmannii* groups; and 2—The *L. melanops* series including species of the *L. boulengeri* and *L. rothi* complexes (= *telsen* group, Abdala 2007a), plus *L. donosobarrosi* and *L. fitzingerii* complexes (= *goetschi* group, Abdala 2007a; Abdala and Quinteros 2014). The four groups within the *L. nigriceps* series are clearly defined and their monophyly consistently inferred and very recently using genomic data, Morando et al. (2020) proposed strongly supported relationships among them; whereas the four complexes within the *L. melanops* series (some of them also referred as groups) are not consistently inferred as clades in available studies. Although relationships among these main eight groups or complexes and within the four of the *L. melanops* series are still discordant (see Chap. 9 for possible causes), we summarize taxonomic information following the preceding organization.

***Liolaemus nigriceps* Series**

The *Liolaemus anomalus* group was first recognized by Cei (1986), but after several years of taxonomic rearrangements, Abdala (2007a) revised the group to include four species. More recently, Abdala and Juárez Heredia (2013) revised the taxonomic history of the group, and reassessed relationships based on a cladistic analysis with morphological characters; they described three new species. These authors also compiled the taxonomic history of this small group, showing that it is probably one of the most complex within the genus. The seven described species are stout, medium-sized lizards (maximum SVL 66.7–92.6 mm), with large heads, short tails, and slim legs. All are oviparous, insectivorous, with cryptic coloration, and found mainly in lowlands and arounds salt-pan flats in Monte Province environments. Some species are known only from a few localities, e.g., *L. pipanaco* (Abdala and Juárez Heredia 2013) or *L. ditadai* (Abdala 2007b; Avila et al. 2015b). As a clade they are one of the least-known of the genus; they are poorly represented in biological collections and almost nothing is known of their natural history. This species group is represented in Patagonia by a single species, *Liolaemus lentus* (Fig. 7.15). This species was described by Gallardo (1966b) but soon synonymized without a clear motive by Donoso-Barros (1969), and resurrected again by Abdala (2007a). *Liolaemus lentus*, as all other species of the group, is a small but stout terrestrial *Liolaemus*, and does not exhibit an evident sexual dimorphism. Its habitat is confined to arid surroundings of salt-pan flats of the Monte Province. Only a few localities are known for the species, the original type locality of Gallardo (1966b), citations by Abdala and Juárez Heredia (2013), Pérez and Avila (2011), and an observation report by Rodríguez Mira et al. (2013) in the Lihue Calel National Park, La Pampa province.

The *Liolaemus darwinii* group is a clade of 21 small species (maximum SVL 61–70 mm but almost 90 mm in *L. irregularis* and *L. albiceps*), that inhabit typical Monte Province environments and some ecotonal regions in central-west Argentina. A subclade of highlands viviparous species inhabit Puna environments, but almost all species from lowlands are terrestrial (ground-dwelling), oviparous, mostly insectivorous, and usually display a well-marked sexual dimorphism. Three lowland species are known in Patagonia: *Liolaemus darwinii* (Fig. 7.16b, c), *L. grosseorum* (Fig. 7.16c, d), and *L. parthenos* (Fig. 7.17a). *Liolaemus darwinii* and *L. grosseorum* are exclusive to the Monte Province environments with sandy or loose soils, but *L. parthenos* is found in an ecotonal formation with Patagonian Steppe vegetation. Taxonomic studies of this group began with Etheridge (1992, 1993), who split the nominal "*L. darwinii*" into several new species, mainly distributed in the northern

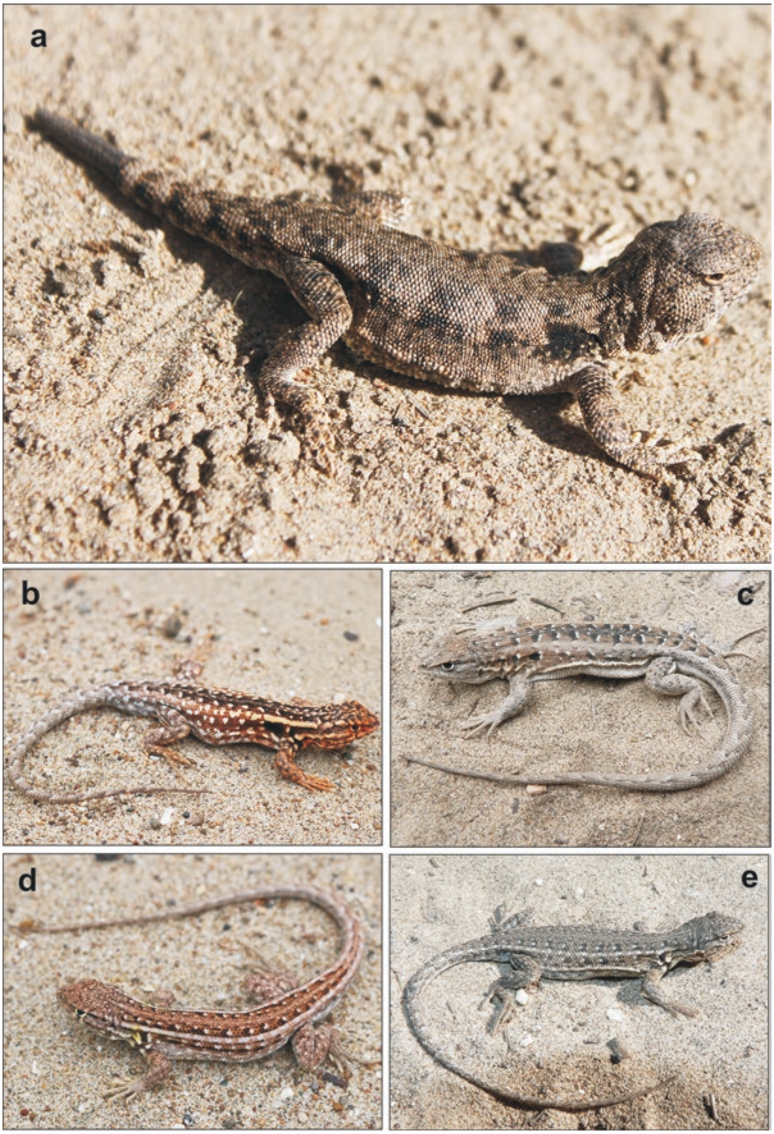

Fig. 7.16 *Eulaemus*. (**a**) *Liolaemus lentus*, from Río Negro Province, Argentina. A rare lizard inhabitant of salt pan flats areas and the southernmost member of the *Liolaemus anomalus* species group, (**b**) *Liolaemus darwinii* male, (**c**) female, showing the marked sexual dichromatism, (**d**) *Liolaemus grosseorum* male, (**e**) female

Monte Province. Etheridge (2000) later added *L. grosseorum* to this clade, and recently Abdala et al. (2016) described *L. parthenos* as the first parthenogenetic species of the Pleurodont iguanian. Updated revisions on the geographic distribution, evolution, phylogeny, and phylogeography of this group were published by Abdala (2007a), Morando et al. (2004, 2008), and Camargo et al. (2012a, b, 2013).

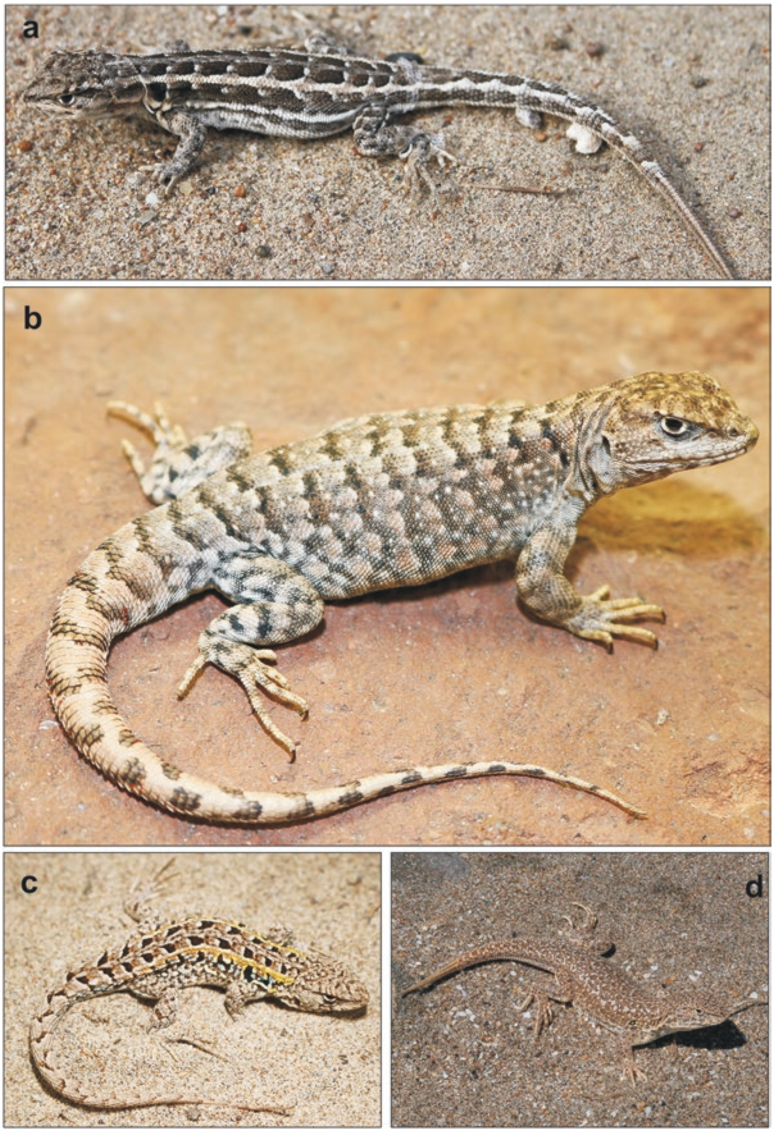

Fig. 7.17 *Eulaemus*. (**a**) *Liolaemus parthenos*, the unique alleged parthenogenetic *Liolaemus*, (**b**) *Liolaemus duellmani*, the only member of the *Liolaemus montanus* species group in Patagonia, (**b**) *Liolaemus wiegmannii*, (**c**) *Liolaemus multimaculatus* (Courtesy of J.W. Williams)

The *Liolaemus montanus* group (Olave et al. 2014) is comprised of at least 64 species ranging from northern Argentina and Chile, and north into Bolivia to central Perú. Species in the clade inhabit environments from near sea level to more than 5000 m a.s.l. (Aguilar et al. 2017, 2018). Members of this clade occupy the highest known altitude in the Americas, and probably the world; a population of an unidentified species is documented at 5176 m a.s.l. in the Bolivian Andes (Aparicio and Ocampo 2010). All species are terrestrial, viviparous or oviparous, usually with little sexual dimorphism; species are small- to medium-sized (maximum SVL 85.0–99.2 mm, Abdala et al. 2008), with stout bodies, and extensive color polymorphism. This is one of the largest groups of *Liolaemus*, but given its species diversity and huge geographic distribution, it is vastly understudied. Not surprisingly this clade is characterized by a confusing taxonomic history with species descriptions and synonymies, but also likely with much yet-to-be-discovered diversity. Phylogenetic relationships within the group are still poorly understood, Lobo et al. (2010c) proposed some grouping but only Aguilar et al. (2015) have provided solid evidence for the monophyly of some groups. Within this large group only *Liolaemus duellmani* (Fig. 7.17b), a microendemic in southern Mendoza province, inhabits Patagonian Province environments. This species is a very poorly studied, the only data available are from its original description (Cei 1978). According to Lobo et al. (2010c), this species is part of an *L. andinus* clade, but further study is needed based on sampling throughout the geographic range of this clade. To our knowledge, only a few lizards have been collected since the original description, and the pictures included in this chapter are the first color photograph ever published for the species.

The *Liolaemus wiegmannii* group is a 12-species clade of small (maximum SVL = 60–85 mm) psammophilous, oviparous, and insectivorous lizards, well supported by morphological, behavioral, and molecular studies (Etheridge 1995, 2000; Schulte et al. 2000; Avila et al. 2006, 2009; Olave et al. 2014; Villamil et al. 2019). Species of the group have a broad geographic distribution across Argentina, Paraguay, Brazil, and Uruguay. In fact, they are the only representatives of *Liolaemus* in these last two countries. In the area covered by this work, the group is represented only by four species: the broadly but patchy-distributed *Liolaemus wiegmannii* (Fig. 7.17c), and the strictly psammophilous *L. multimaculatus* (Fig. 7.17d), *L. cuyumhue* (Fig. 7.18a), and *L. rabinoi* (Fig. 7.18b). *Liolaemus wiegmannii* is a relatively common species distributed through several provinces in Argentina and the south-west, south, and east shores of Uruguay (Etheridge 2000; Villamil et al. 2019). Across this extensive range, the species occupies a diversity of sandy habitats and sedimentary outcrops. In Mendoza and some localities of Río Negro and La Pampa, *L. wiegmannii* is observed in sandy soils and small dunes surrounded by Monte Province vegetation, or ecotonal areas between Monte and Espinal Provinces. It is also found along the Atlantic coastal dunes along the north shores of San Matías Gulf (Vega and Bellagamba 1994; Pérez et al. 2011), and apparently going inland through the Negro River Valley (Stellatelli et al. 2014). *Liolaemus wiegmannii* is a species complex that includes some disjunct populations that likely represent independent lineages (Villamil et al. 2019). *Liolaemus multimaculatus* occupies Atlantic coastal dunes in Buenos Aires and northern Río Negro provinces (Vega and Bellagamba 1994; Etheridge 2000). Its westernmost distribution is Villarino Point in the mouth of the San Antonio Bay (LJAMM-CNP 16643). Populations south of the Buenos Aires coastal sand dunes system extend to the northern shore of the San Matías Gulf, but apparently the population's density is lower than that along the

Fig. 7.18 *Eulaemus*. *Liolaemus cuyumhue* (**a**) and *L. rabinoi* (**b**) two of the most endangered species of *Liolaemus* from Patagonia

Buenos Aires coast. However, no extensive surveys have been carried out in its southern distribution. *Liolaemus rabinoi* was described by Cei (1974b) based upon two adult specimens collected on the shores of El Nihuil dam, near the Club de Pescadores, San Rafael Department, Mendoza Province, Argentina (Fig. 7.18b). For almost 35 years *L. rabinoi* was cited as probably extinct based on the lack of new collections around the type locality, but the species was recently rediscovered and redescribed by Abdala et al. (2017). *Liolaemus cuyumhue* was described by Avila et al. (2009) from a unique locality in a closed basin in eastern Neuquén province, known as Bajo del Añelo (Añelo Basin) in northern Patagonia (Fig. 7.18a). As with *L. rabinoi*, *L. cuyumhue* is found only in a few localities clustered near each other, and almost all natural history information is anecdotal. Both species have been recently classified as Critically Endangered by the IUCN: *L. rabinoi* is threatened by "off-road" recreational activities (motorbikes or ATVs; "all-terrain vehicles"), in its very localized dune field habitat. *Liolaemus cuyumhue* is restricted to the core of the Vaca Muerta gas and oil production area, where large-scale extraction by the controversial "fracking" methodology is destroying large areas of natural habitat without any apparent control. These two species are probably the most endangered species of the entire genus at the time we write this (Chap. 14), but almost all species of this clade, except perhaps the *L. wiegmannii* populations (but see Villamil et al. 2019), have some serious conservation problems.

The *Liolaemus melanops* Series

Several groups/complexes have been proposed within this series, but phylogenetic relationships are still uncertain (Chap. 9). The *Liolaemus boulengeri* complex is a group of small species (maximum SVL 70–75 mm), terrestrial, oviparous, insectivorous, and with some degree of sexual dimorphism, occurring mainly in Patagonian Province steppe environments (Fig. 7.19). Presently, this group includes five described species: *Liolaemus boulengeri*, *L. senguer*, *L. inacayali*, *L. tehuelche*, and *L. telsen*. *Liolaemus boulengeri* Koslowsky 1898 was, until a few years ago, thought to have one of the largest distributions of all Patagonian lizards, but several recent studies (Abdala 2003, 2005, 2007a; Avila et al. 2006) showed that in fact this group was a species complex, and some species are now recognized as part of the *Liolaemus boulengeri* group. Abdala (2005) redescribed the nominal species and suggested an approximate type locality, and identified additional “candidate species” that are still undescribed (Abdala 2007a; Avila et al. 2006; Olave et al. 2014). Some sampled populations of western Chubut do not yet include males, and may be another case of parthenogenesis (only the second documented) in Pleurodont Iguanian lizards. This must be corroborated with an adequate sampling effort and an integrative study (as with *Liolaemus parthenos*; Abdala et al. 2016).

The name *Liolaemus donosobarrosi* group was coined by Cei (1986) to include only the species *Liolaemus donosobarrosi*, initially described by Cei (1974b) as part of the genus *Ctenoblepharys*. Avila et al. (2006) expanded this study by including *Liolaemus cuyanus* and several then undescribed species, two of which are now named: *L. calliston* and *L. tirantii* (Fig. 7.20) (Avila et al. 2017). Abdala (2007a) resolved the *L. donosobarrosi* group as paraphyletic (mainly using morphological characters) and did not recognize it, but Abdala and Quinteros (2014) recognized a *L. cuyanus* clade including *L. cuyanus*, *L. donosobarrosi*, *L. goetschi*, and *L. mapuche*.

Recent papers by Fontanella et al. (2012) and Olave et al. (2014, 2015) inferred this group as monophyletic, and we follow this hypothesis here. This small group is characterized by a large range of body sizes (maximum SVL 60–90 mm), morphology, and coloration, we recognize the following species as part of this group: *Liolaemus cuyanus*, *L. donosobarrosi*, *L. calliston*, *L. tirantii*, *L. josei*, *L. puelche*, and *L. mapuche* (Figs. 7.20 and 7.21) as well as at least six potential candidate species (Olave et al. 2014). As a group these lizards are terrestrial, oviparous, and insectivorous, and some seem to be restricted to limited environments, as *L. cuyanus* or *L. mapuche*, apparently only found in Mediterranean dunes. *Liolaemus puelche* was described by Avila et al (2007b), but it is known only from one locality. *Liolaemus calliston* is sympatric with *L. cuyumhue* and, as with some other species, will be probably critically endangered soon by oil and gas extraction activities (Chap. 14). This species was only very recently described (Avila et al. 2017), its

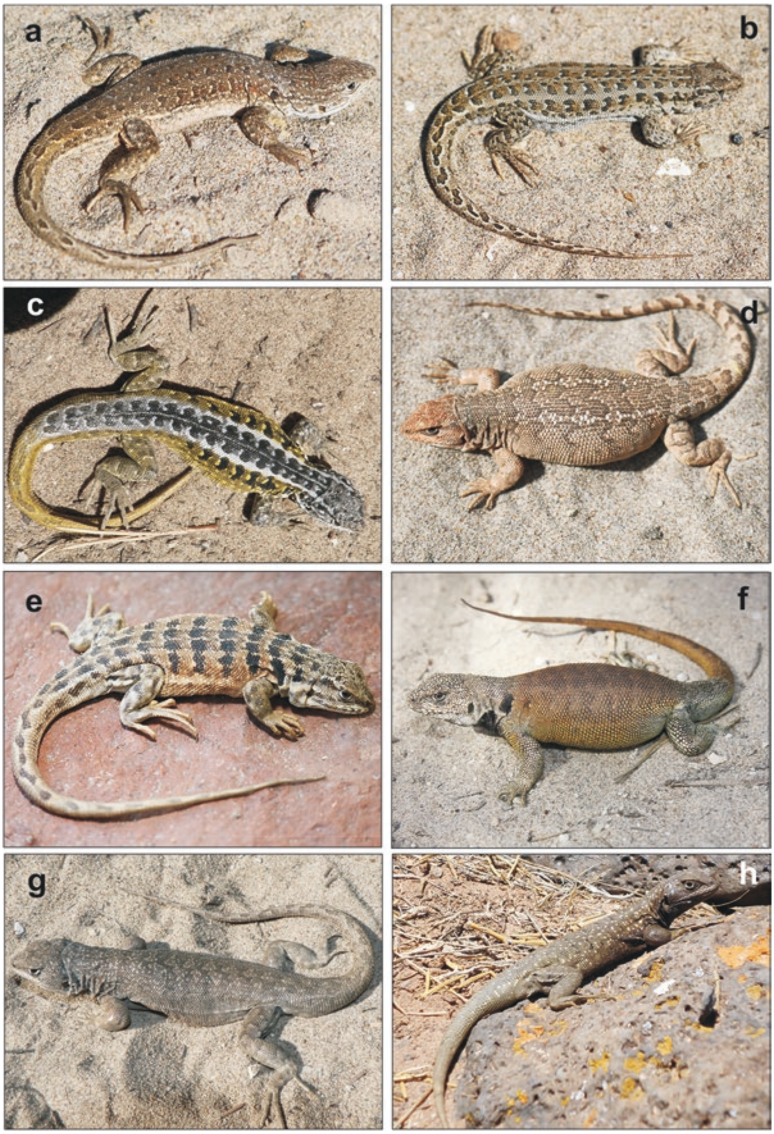

Fig. 7.19 *Eulaemus*. (**a**) *Liolaemus boulengeri*, (**b**) *Liolaemus senguer*, (**c**) *Liolaemus telsen*, (**d**) *Liolaemus rothi*, (**e**) *Liolaemus hermannunezi* (TL), (**f**) *Liolaemus tromen*, (**g**) *Liolaemus sagei* (TL), (**h**) *Liolaemus sitesi* (TL)

conservation status has not been evaluated. All species are known only from Monte Province environments and all, except *L. cuyanus*, are endemics to the region covered by this book.

The *Liolaemus fitzingerii* group (Fig. 7.22) is broadly distributed in coastal and Patagonian shrub-steppe habitats along extra-Andean Patagonia. This group is

Fig. 7.20 *Eulaemus*. (**a**) *Liolaemus cuyanus*, (**b**) *Liolaemus mapuche* (TL), (**c**) *Liolaemus josei* (TL), (**d**) *Liolaemus goetschi* (TL), (**e**) *Liolaemus calliston* (TL)

morphologically diverse, species range in maximum size (snout-vent length [SVL]) from 74.2 (*L. goetschi*) to 110 mm (*L. fitzingerii*; Abdala et al. 2012a, b), and sexual dichromatism is absent in some species and very evident in others. This species group was first proposed by Cei (1979) as one of the major evolutionary units among Patagonian lizards. Cei (1979) was the first to note that the color variation

Fig. 7.21 *Eulaemus*. (**a**) *Liolaemus tirantii*, (**b**) *Liolaemus purul*

was a source of taxonomic confusion in some species, and made several contributions to the study of this group with A. Scolaro (Cei 1986 and Abdala 2007a, for a review of taxonomic history). Currently, 12 species have been described within the *L. fitzingerii* group (Etheridge and Christie 2003; Abdala 2007a; Abdala et al. 2010, 2012a, b; Avila et al. 2006, 2008, 2010b): five in the *L. fitzingerii* complex (*L. camarones*, *L. chehuachekenk*, *L. fitzingerii*, *L. shehuen*, and *L. xanthoviridis*), and six in the *L. melanops* complex (*L. casamiquelai*, *L. dumerili*, *L. goetschi*, *L. martorii*, *L. melanops*, and *L. morenoi*). Taxonomy of the *L. fitzingerii* group has been muddled since the first species description in the early nineteenth century. As for all other groups, species were originally described solely on morphological characters (e.g., *L. dumerili* and *L. purul*, Abdala et al. 2012b; *L. camarones* and *L. shehuen*, Abdala et al. 2012a). Some of these characters are related to color pattern and melanism, the latter of which was shown to be uninformative for delimiting species in this group (Escudero et al. 2012). More recently species have been described on the basis of both molecular (generally mtDNA) and morphological characters (e.g., *L. chehuachekenk*, Avila et al. 2008; *L. casamiquelai* Avila et al. 2010b).

Fig. 7.22 *Eulaemus*. (**a**) *Liolaemus fitzingerii*, (**b**) *Liolaemus xanthoviridis*, (**c**) *Liolaemus canqueli*, (**d**) *Liolaemus shehuen*, (**e**) *Liolaemus melanops*, (**f**) *Liolaemus morenoi* (TL), (**g**) *Liolaemus casamiquelai*, (**h**) *Liolaemus chehuachekenk* (TL)

Relationships inferred from mtDNA and morphological characters are often in stark contrast to one another (e.g., Avila et al. 2006; Abdala et al. 2012a, b; Grummer et al. 2018). As noted above, external morphological characters such as color and pattern are highly variable within species, and melanism, a character used in the original diagnoses of many *L. fitzingerii* group species, varies ontogenetically between males and females (Escudero et al. 2016). Minoli et al. (2014) did not find support for recognition of *L. camarones* as a distinct species, based on an integrative approach combining morphological and envelope niche modeling, and Grummer (2017) could not differentiate this species with genomic data. Olave et al. (2014) included representatives of all species of the *L. fitzingerii* group in a molecular study (14 loci) of the subgenus *Eulaemus*, and failed to find strong support for most relationships. A genomic study that included 12 species of this group (Grummer et al. 2018) failed to find support for most of the relationships among them. Grummer et al. (2018) did infer a well-supported (*L. fitzingerii* + *L. xanthoviridis*) clade, but also inferred several instances of reticulation (Chapter 9 briefly explains the extent of hybridization within species of this group). A comprehensive species delimitation study with finer-scale sampling would be necessary to fully test the species-level status of both described and "candidate species" taxa in the *Liolaemus fitzingerii* group. Grummer et al. (2018) found that the level of molecular diversity in the *L. fitzingerii* species group is similar to other lizard species "complexes" in which one to a few species are recognized. The *Liolaemus rothi* group was created by Cei (1986) to include a couple of species of stout lizards only found in the Patagonian Province steppe region of Argentina; these lizards were initially assigned to the *Liolaemus fitzingerii* complex by Cei (1979). But the original description of *Liolaemus rothi* was ambiguous; a careful study by Etheridge and Christie (2003) included a species redescription and a proposal for a type locality area. At the present time, six species are included in the group, but a few others will probably be added soon. With the exception of the nominal species of the group, all others were described after 2000. Olave et al. (2017) used the name *Liolaemus rothi* complex (Fig. 7.19), for the group including *L. rothi*, *L. sagei*, *L. hermannunezi*, *L. tromen*, *L. sitesi*, and *L. loboi*, plus two candidate species previously hypothesized by Olave et al. (2014; *L.* sp. 4) and Morando (2004; *L.* sp. M34). *Liolaemus purul* (Fig. 7.21) was recently described as part of the *L. melanops* series (Abdala et al. 2012a; Abdala and Quinteros 2014), and we consider it as part of this complex (unpublished data). Little more than the original descriptions are available for these species in the literature, and the last and most recent publication on current species limits of this group is Olave et al. (2017); but high levels of introgression have been detected among *L. rothi* and various species of the *L. boulengeri c*omplex, which may be blurring species boundaries (Olave et al. 2018).

7.3 On the Type Localities of Patagonian Lizards

The International Code of Zoological Nomenclature (ICZN) mandates that the collection site of the name-bearing type of a nominal species be designated as the type locality of the taxon described. By this criterion the type localities for Patagonian lizards are clearly established for only some species. Usually in the descriptions throughout the last two decades, the type locality is accurately described when clear geographical reference points, maps, and geographic positioning devices (GPS) are available; this increases the possibility for very precise map to appear in original species descriptions.

In the earlier times, the nineteenth century, specimen collectors and "species descriptors" were often not the same person, the majority of the descriptions did not have very accurate type localities, and it is often difficult to reconstruct where type specimens were collected. As an example, Koslowsky's descriptions of Patagonian lizards (Koslowsky 1896, 1898) do not have any clear description of type localities, but some herpetologists were able to establish approximate type localities for some species. Examples include Etheridge and Christie (2003) for *Liolaemus rothi*, Abdala (2005) for *Liolaemus boulengeri*, and Lobo and Quinteros (2005a) for *Phymaturus patagonicus*. A similar historical reconstruction made by Etheridge (1998) for *Liolaemus hatcheri*, which was described for an undisclosed locality of Santa Cruz province by Stejneger (1909), was based on a third-party collector. Cei (1998) was able to reconstruct the most probable type locality for *L. melanops* for Sierra Colorada hills in Chubut province. We found that the type locality area for *L. elongatus* is in western Chubut, using a combination of distributional data and phylogenetic information, as well as we are redescribing the species (Avila, unpublished data).

Surprisingly some species collected by the H.M.S. Beagle expedition in the early nineteenth century have a well-established type locality, for example Port Desire, now known as Puerto Deseado, a small city in the Atlantic coast of northern Santa Cruz province. Species collected there by C. Darwin according to Bell (1843) are: *Liolaemus gracilis*, *L. bibronii*, *L. kingii*, *Diplolaemus bibronii*, and *D. darwinii*. But it is obvious that some error occurred during the trip when sorting the collected specimens, because *L. gracilis* is a species found only in Monte Province environments and not in Patagonian Province, as is Puerto Deseado. In other cases, several types of localities seem to be very difficult or impossible to locate. As an example, *Leiosaurus bellii* was described from "Mexico". This kind of extreme error may originate from a large array of problems, ranging from the original definition involving vast or ambiguously defined areas (as … "territorio del Chubut, cerca de las cordilleras" or "en el Neuquén" for *L. elongatus* Koslowsky 1896); disappearance of original notes (e.g., Koslowsky notes are lost, J.D. Williams, personal communication); lack of maps or topographic references at the time of the original collection; or more commonly, ambiguous or lack of details in the description of the localities or in the maps (if included). For taxonomic studies in the early twentieth century, probably a general description, such as the name of a mountain or mountain range, was enough; but with the rapid growth of knowledge of our diversity that kind of description of the collection site is too basic. Other problems could have originated from oversights in some part of the collection and/or preservation process (e.g., *Leiosaurus bellii*); and, as seen in some recent descriptions, a deliberate attempt to hide the real type locality (as has been the case with some researchers), an action supported by conservationists to avoid illegal collection for the "pet trade".

Unfortunately, when attempting to resolve taxonomic problems, it is of crucial importance to collect additional specimens at a particular type locality. Whatever the reasons this material is needed for, these specimens must be collected at the type locality of the status of taxon in question. As such, the value of knowing the exact collection sites of what later become type specimens is clear for all those interested in taxonomy. Researchers must contribute an accurate description of the geographical site, including GPS coordinates with the maximum detail and/or accurate maps, and ideally photos.

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Chapter 8
Biogeography, Ecology, and Spatial Patterns of Patagonian Lizards

Ignacio Minoli, Cristian Hernán Fulvio Pérez, Mariana Morando, and Luciano J. Avila

Abstract Patagonia has a great diversity of lizards, including 6 families, 11 genera, and 163 species. The majority of this diversity with documented geographical records corresponds to the Liolaemidae family (*Phymaturus* and *Liolaemus*). Latitudinally, lizard richness is higher between 37° and 39° S, decreasing gradually until latitude 54° S; longitudinally, it is higher between 69° and 71° W. The georeferenced records and the number of collected specimens have some biases, with higher values in the northern regions (up to latitude 42° S). However, there are areas up to latitude 45° S with species richness similar to others with a greater number of collected individuals. The vegetation units with the highest species richness (*S*) in Argentinean Patagonia are the northern and central areas reaching west of Chubut Province: Western District ($S = 60$) and Typical Southern Monte ($S = 49$), passing through areas with intermediate richness and with only one species (Wet Magellanic Steppe) or none (Evergreen shrub, Monte's Mountains and Valleys, Western Interior Pampa, and Peat Bogs). There is a general trend toward lower species richness in vegetation units located in the extreme south of Argentina and south of latitude 41° S in Chile. We evaluated differences in lizard diversity and evenness among vegetation units through a dendrogram based on species incidences and found six clusters. Then, we compared species richness between members of each cluster with rarefaction curves. Species marginally distributed in Patagonia have a narrower altitudinal range than Patagonian endemics. Species in genus *Liolaemus* have small differences in altitudinal range, but species of *Phymaturus* have pronounced differences in altitudinal ranges. Our spatial analyses, based on intensive systematic-taxonomic activity over the last two decades, shed light into the understanding of lizard distributions in one of the regions with the greatest diversity of reptiles in the world. We

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I. Minoli (✉) · M. Morando · L. J. Avila
Instituto Patagónico para el Estudio de los Ecosistemas Continentales – Consejo Nacional de Investigaciones Científicas y Técnicas (IPEEC-CONICET), Puerto Madryn, Chubut, Argentina
e-mail: minoli@cenpat-conicet.gob.ar; morando@cenpat-conicet.gob.ar; avila@cenpat-conicet.gob.ar

C. H. F. Pérez
UAT, CCT-CONICET CENPAT, Puerto Madryn, Chubut, Argentina

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also provide ecological and spatial metrics for an updated list of Patagonian lizards. We highlight that the usefulness of discretizing large volumes of information and geographic space into a synthetic framework allows using quantitative results for the study of spatial patterns of biodiversity, decision-making for design studies, use of resources, and creation of protected areas.

Keywords Geographic · Distribution · Range · Diversity · Lizards

8.1 Biogeography and Ecological History

The biogeography of a region is defined by the study of organisms or species' distributions and ecosystems, taking into account their relationships with the geographical space and geological periods (Cox and Moore 2010). The applications of biogeography and its constant changes through time and spatial scales, are not only limited to knowing where species inhabit, but have a very important role in public health, economic production, environmental assessment, sustainable use of resources, landscape planning, and conservation management (Spellerberg et al. 1999). In a more general context, biogeographical studies help us to understand the processes associated with the origin and maintenance of distributional patterns (Sanmartín 2012). Geological and climatic processes could affect biological characteristics through time such as reproduction (Pyron and Burbrink 2014; Liang et al. 2018), trophic level (Pianka 1986; Cooper 1997), body size (Pincheira-Donoso et al. 2008), and even the emergence of new species (Pincheira-Donoso et al. 2015). This strong relationship between species diversity and climatic and geological history makes Patagonian lizards an interesting object for biogeographical studies.

Knowledge of the geological and climatic events that occur over time in an area is essential to understand the processes that led to differences in biodiversity among different regions of the planet (Morrone 2001a). In the Patagonian region, the distribution of species' assemblages has been shaped by two important geological-climatic events: the orogeny of the Andes (Middle-Late Miocene ~15–10 Ma) and the Pleistocene Glaciations (~ 2.5 Ma 11.7 ka) (Paruelo et al. 1998; Morrone 2001b; Albino 2011; Ruzzante and Rabassa 2011). The Andean orogeny introduced an important rain shadow toward the east, creating a cold and dry climate throughout the Patagonian steppe that promoted a reduction of South American forests in the southern sector and the expansion of taxa adapted to xeric environments (Barreda and Palazzesi 2007). Although Patagonian glaciations began at the end of the Miocene, the Patagonian ice sheet reached its full development during the early Pleistocene (Rabassa 2008). These glacial advances were represented with great impact in this region, such as the Great Patagonian Glaciation (GPG, 1–1.2 Ma) and the Last Maximum Glacial (LGM, 21 ka). In comparison with the LGM and other Pleistocene glaciations in the Patagonian Steppe, the GPG turned out to be the maximum expansion of the ice sheets (Rabassa 2008) and paleoenvironmental reconstructions allow us to know that the amount of terrestrial area in the past was very different from the current one (Ponce et al. 2011). Glaciations in Patagonia produced sea-level changes, exposing part of the continental shelf in the east and considerably increasing the available geographical space for colonization by plants and animals (Ponce et al. 2011), and promoted latitudinal movements of major ecosystems (Rabassa and Coronato 2009). The increase in extreme temperatures, aridification of the surrounding areas, decrease in precipitation, and the absence of the sea conditioner effect that displaced its coastline to the east (Rabassa and Coronato 2009) were factors that influenced the high-latitude biota of Patagonia, even in areas that were not encompassed by glaciers. However, substantial areas remained free of ice during glacial episodes and climatic conditions were less severe than those of North America (Markgraf et al. 1995). The climatic history has a strong relationship with the creation of biomes in the Patagonian region (Markgraf et al. 1995).

Biomes or ecological regions are defined as relatively large biogeographical areas distinguished by their unique climate, soils, hydrology, ecology, flora and/or fauna, and intended to serve as a geographic organizational tool for ecosystem management (Clements and Shelford 1939; Sodhi and Ehrlich 1995; Burkart et al. 1999). From an ecological historical point of view, these are strongly cohesive units, large enough to cover the ecological processes or the life history for most of the species that inhabit and interact therein (Sodhi and Ehrlich 1995). The spatial relationship between lizard species and these ecological units is one of the main axes in the analyses carried out for this chapter. Here we used discrete spatial subsamples, consisting of hexagonal, latitudinal–longitudinal, and vegetation zoning units, to (1) analyze patterns of richness, diversity, density, and number of sampling geographical records, and (2) analyze altitudinal patterns between genera and species.

8.2 Study Area

The area considered as Patagonia for this chapter is located between 33°53′48.62″ S–55°58′55.71″ S and 75°41′27.83″ W–62°06′31.39″ W, covering approximately 1,305,870 km^2 (~ 7.38% of South America) and corresponding to central–southern Argentina and Chile (Fig. 8.1a). Based on a coarse classification, the study area can be divided into a cold, humid, mountainous Andean-Patagonian forest region in the west, and the Patagonian steppe region, which extends widely eastwards to the Atlantic Ocean and is mostly low, cold, dry and characterized by scattered grasses and shrubs (Cabrera 1976; León et al. 1998). Patagonia can be defined as a temperate or cool-temperate region and presents a characteristic NW-SE temperature pattern, determined mainly by the presence of the Andes. Local factors such as topography and wind affect air temperature. The climate is dry and cold in most of the territory, with an extremely variable temperature ranging from −30 °C in the winter to 45 °C degrees in the summer (Chap. 3).

The influence of the Pacific air masses and the Andes as a topographic barrier parallel to the Pacific coast results in a strong west-east gradient of precipitation

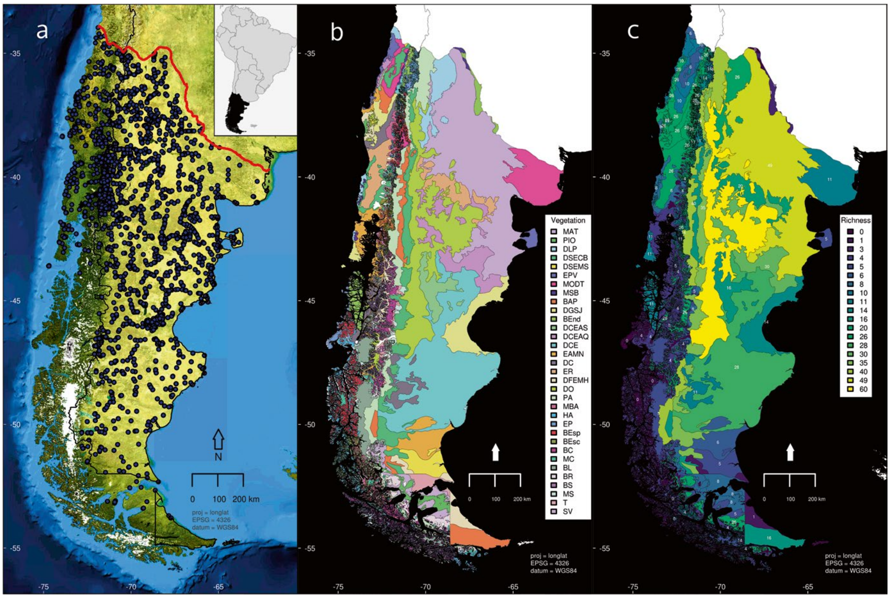


Fig. 8.1 (**a**) Patagonian region and lizard's georeferenced records reviewed for this study. (**b**) Vegetation divisions used in this study following the proposal of Luebert and Pliscoff (2017) and Oyarzabal et al. (2018). (**c**) Lizard's species richness by vegetation units. References: Endorheic Bolsons = BEnd, Deciduous Forest = BC, Sclerophyllous Forest = BEsc, Thorny Forest = BEsp, Laurel Forest = BL, Resinous Forest = BR, Evergreen Forest = BS, Andean—Patagonian Forests = BAP, Central District = DC, Erial Central District = DCE, Central District—Quilenbai steppe bushes = DCEAQ, Central District—Mountain steppe bushes = DCEAS, Payunia District = DLP, San Jorge Gulf District = DGSJ, Fueguino District—Wet Magellanic Steppe = DFEMH, Western District = DO, Sub Andean District—Steppe of white coiron = DSECB, Sub Andean District—Dry Magellanic Steppe = DSEMS, Valdés Península Ecotone = EPV, Rionegrino Ecotone = ER, Shrub steppe of black bush = EAMN, Steppes and pastures = EP, Altitude grass = HA, Low altitude scrub = MBA, Deciduous scrub = MC, Evergreen shrub = MS, Typical southern Monte = MAT, Monte's Mountains and Valleys = MSB, Eastern or Transitional Monte = MODT, Western Interior Pampa = PIO, Altoandina Province = PA, Peat Bogs = T, and Without vegetation = SV

across the region (Barros et al. 2015). The rising air cools faster on the west side of the Andes, originating an annual rainfall exceeding 2000 mm on the Chilean side. On the eastern side of the Andes, the total annual precipitation decreases exponentially and most of the central portion of Patagonia receives less than 200 mm per year (Paruelo et al. 1998). Additionally, there are large areas that are annually affected by fallen snow and permanent ice fields. The different patterns of temperature, soil type, precipitation, and geological history have shaped different types of vegetation that prevail today in this broad region (Morello et al. 2012).

Patagonia had major changes since the 1890s and has undergone steady change as a result of human activity, but there has been no clear understanding of the resulting effects on biodiversity. Over the twentieth century, business activities such as oil extraction, mining, and ranching have affected different ecosystems of this area. In particular, sheep overgrazing (Bisigato and Bertiller 1997; Cesa and Paruelo 2011) has led to desertification in the vast semiarid portion of Patagonia (Ares et al. 1995; Aguiar et al. 1996). Another factor that may affect the diversity and ecological dynamics of large xerophytic areas like Patagonia (e.g., Schulze et al. 1996) is the creation of hydroelectric dams, which implies anthropic management of regional water availability and seasonal changes in rainfall (Paruelo et al. 1998) or river flow rates (Masiokas et al. 2008). An overall analysis of lizard diversity based on accurate species distributional data is essential for understanding the impact and consequences of these types of human activity (Böhm et al. 2013; Cook et al. 2013).

8.3 Methods

8.3.1 Data Collection

We carried out extensive biological surveys that began in early 1998 and continued until 2018, with field trips made in different representative areas of the Patagonian region. Throughout these decades of fieldwork, we sampled different ecoregions and completed gap areas without previous records. Each record has a voucher number with a species identity assigned, date, and place of origin. Collection sites were geographically referenced using a Garmin GPS 12TM Global Position Device. The systematic classification for families was according to Oppel (1811), Gray (1827, 1865), Frost et al. (2001), and Gamble et al. (2008). Specimens were deposited or consulted in several herpetological collections (Fig. 8.2a): LJAMM-CNP (IPEEC-CONICET), BYU (Monte L. Bean Museum, Brigham Young University), MLP (La Plata Museum), and FML (Miguel Lillo Foundation). Additional museum collections, literature vouchered, and GBIF records were obtained from AMNH (American Museum of Natural History, USA), APN-AR (Administration of National Parks Argentina), CAS (California Academy of Science, USA), CH (Colección Centro Regional Universitario Bariloche, Universidad Nacional del Comahue, Río Negro,

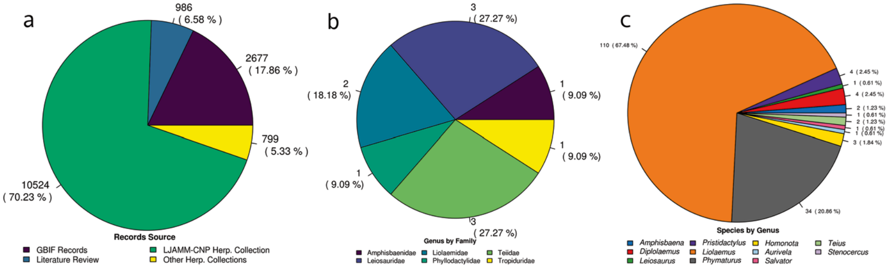


Fig. 8.2 (**a**) Information sources from the georeferenced records used for analysis in this chapter. (**b**) Number of genera by family. (**c**) Species number by genus

Argentina), CHDPD (Colección personal Daniel Pincheira-Donoso), CNHM (Chicago Natural History Museum; in the present The Field Museum of Natural History, FMNH, USA), CRILaR (Centro Regional de Investigaciones Científicas y Transferencia Tecnológica, Argentina), CTALA_LB (Ministerio del Medio Ambiente de Chile), FBC (Félix Benjamín Cruz Field Collection, Argentina), IADIZA (Instituto Argentino de Investigaciones de las Zonas Áridas, Argentina), IBA-UNC (Universidad Nacional de Cuyo, Argentina), JAS-DC (José Alejandro Scolaro, Centro Nacional Patagónico, Puerto Madryn, Argentina), JMC-DC (Colección Herpetológica José Miguel Cei, Argentina), KU (Kansas University reptile collection, USA), MACN (Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Argentina), MCN (Museo de Ciencias Naturales, Universidad Nacional de Salta, Argentina), MCZ (Museum of Comparative Zoology, Harvard University, USA), MHNG (Muséum d'histoire naturelle de la Villede De Genève, Switzerland), MLP (Museo de la Plata, Argentina), MNHN (Museum National de Histoire Naturelle, France), MNHNC (Museo Nacional de Historia Natural, Chile), MNW (Muzeum Narodowe w Warszawie, Poland), MVZ (University of California at Berkeley, USA), MZUC (Museo de Zoología de la Universidad de Concepción, Chile), NMBA (Zoologische Expedition des Naturhistorischen Museums Basel), OMNH (Osaka Museum of Natural History, Japan), PT (Proyecto *Tupinambis*, Félix Benjamín Cruz, Argentina), RBINS (Royal Belgian Institute of Natural Sciences, Belgium), SDNHM (San Diego Natural History Museum, USA), SDSU (San Diego State University, USA), SMNS (Staatliches Museum für Naturkunde, Germany), SSUC (Colección Patricio Sánchez Reyes de la Pontificia Universidad Católica, Chile), TCWC (Texas A & M University, USA), UNMDP (Colección Herpetológica de la Universidad Nacional de Mar del Plata, Argentina), UWBM (Burke Museum, University of Washington, USA), and ZSM (Zoologische Staatssammlung, Germany). Literature and museum records with acronyms or specific localities were quoted literally.

8.3.2 Spatial Analyses

We constructed a hexagonal grid with 1122 cells (White et al. 1992; White 2000) with a hexagon average area of 1163.5 km^2, covering the entire territory of Patagonia (Fig. 8.3). We used hexagons rather than squares because they possess greater statistical efficiency (Olea 1984) and are more dynamically adaptable (Yfantis et al. 1987), allowing them to adjust to the boundaries of a highly irregular perimeter (such as Patagonian Pacific and Atlantic coastlines). In this approach with continuous tessellations, hexagons have the advantage over squares in that all six adjacent sides are equally distant, while squares have four closer and four more distant neighbor sides (Dengler 2009). This facilitates the comparison of different and large data sets by discretizing a major and continuous area (White 2000).

Since there are multiple zoning proposals for Patagonian ecoregions (Burkart et al. 1999; Morello et al. 2012) based on plant formations (Roig 1998) and phytogeographic provinces (Cabrera 1994), we decided to use the spatial plant units from

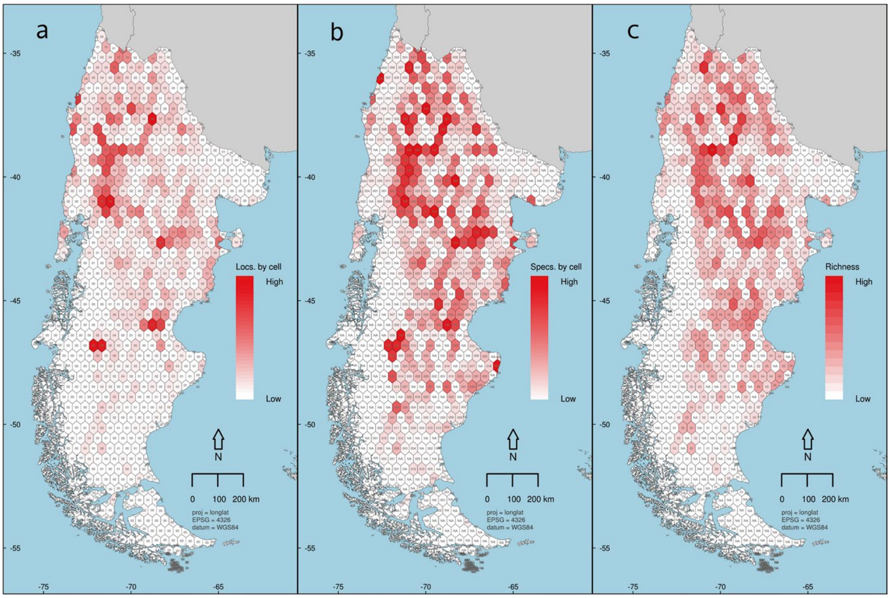


Fig. 8.3 Discrete spatial analysis of Patagonian lizards implementing hexagonal grid cells. (**a**) Number of locations of logs recorded per cell. (**b**) Number of individuals registered per cell. (**c**) Species richness per cell

two of the latest available works on this topic (Luebert and Pliscoff 2017 for Chile; Oyarzabal et al. 2018 for Argentina). These contributions proposed a discretization of Patagonia comprising 33 characterized vegetation units. This refined classification considers the following vegetation units: Endorheic Bolsons = BEnd, Deciduous Forest = BC, Sclerophyllous Forest = BEsc, Thorny Forest = BEsp, Laurel Forest = BL, Resinous Forest = BR, Evergreen Forest = BS, Andean—Patagonian Forests = BAP, Central District = DC, Erial Central District = DCE, Central District—Quilenbai steppe bushes = DCEAQ, Central District—Mountain steppe bushes = DCEAS, Payunia District = DLP, San Jorge Gulf District = DGSJ, Fueguino District—Wet Magellanic Steppe = DFEMH, Western District = DO, Sub Andean District—Steppe of white coiron = DSECB, Sub Andean District—Dry Magellanic Steppe = DSEMS, Valdés Península Ecotone = EPV, Rionegrino Ecotone = ER, Shrub steppe of black bush = EAMN, Steppes and pastures = EP, Altitude grass = HA, Low altitude scrub = MBA, Deciduous scrub = MC, Evergreen shrub = MS, Typical southern Monte = MAT, Monte's Mountains and Valleys = MSB, Eastern or Transitional Monte = MODT, Western Interior Pampa = PIO, Altoandina Province = PA, Peat Bogs = T, and Without vegetation = SV (Fig. 8.1b).

We evaluated the source and overall number of lizard records, and grouped them by families, genera, and species. We used the constructed hexagonal tessellation to obtain the lizards' sampling density (number of localities), density of individuals (number of individuals) and species richness per cell, and assessed their variation latitude, longitude, and vegetation units. We analyzed the species richness number and records by latitude-longitude and by vegetation zonification. Additionally, we performed the Shannon Wiener Index (a diversity metric) and Jaccard's similarity index among the vegetation units. We evaluated the lizard's assemblages per vegetation units through cluster analysis and compared species richness between cluster members with rarefaction curves, to remove the potential bias of uneven catch rates (Gotelli and Colwell 2001; Buddle et al. 2005). Finally, we analyzed the altitude ranges ordered by mean values for all genera and species of *Phymaturus* and *Liolaemus*. All figures, spatial and statistical analyses were performed with R 3.4.4 (R Core Team 2018) and vegan 2.5–2 (Oksanen et al. 2018), tmaptools 1.2–4 (Tennekes 2018), rgdal 1.3–3 (Bivand et al. 2018), rgbif 1.0.2 (Chamberlain et al. 2018), raster 2.6–7 (Hijmans 2017), maps 3.3.0 (Becker and Wilks 2018), geosphere 1.5–7 (Hijmans 2015), SDMTools 1.1–221 (VanDerWal et al. 2014), GISTools 0.7–4 (Brunsdon and Chen 2014), rgeos 0.3–28 (Bivand and Rundel 2018), maptools 0.9–2 (Bivand and Lewin-Koh 2018), sp. 1.3–1 (Pebesma and Bivand 2005), and cluster 2.0.7–1 (Maechler et al. 2018) R packages.

8.4 Diversification and Sampling of Lizards

For 300 years Patagonia has been the stage of herpetological discoveries by naturalists and explorers, from the abbot Juan Ignacio Molina, who made a great contribution to the Chilean fauna with his work "Saggio sulla Storia Naturale del Chili" in 1782, to J. G. Koslowsky (early twentieth century) with great contributions to the exploration of Patagonia's herpetology. Also, great explorers like J. B. Hatcher (1896–1899), F. Meyen (1830–1832), and Charles R. Darwin himself (1833) contributed innumerable materials for the description of the Patagonian herpetofauna by A. M. G. Duméril, G. Bibron, T. Bell, R. P. Lesson, and A. F. A. Wiegmann, among others. In the middle of the twentieth century, herpetologists such as J. M. Cei and J. A. Scolaro explored and sampled large areas of Patagonia and described new species of amphibians and reptiles. In Chilean Patagonia, R. Donoso-Barros conducted numerous and important studies on the herpetofauna. Recently, Patagonia has been visited by many herpetologists and is one of the most explored areas in Argentina, with numerous new species described (see Chap. 1).

We recorded 163 species, 11 genera and 6 families of lizards, obtained from 14,985 distribution records from 2637 unique localities (Table 8.1 and Fig. 8.2). The families with the greatest genera diversity were Teiidae and Leiosauridae, followed by Liolaemidae, Phyllodactylidae, Tropiduridae, and Amphisbaenidae (Fig. 8.2b). We found the highest diversity in *Liolaemus* (110 species) and *Phymaturus* (34), followed by *Diplolaemus* (4), *Pristidactylus* (4), and *Homonota* (3) (Fig. 8.2c).

The number of sampled localities was highest in northwestern Patagonia, between 35°–42° S and 74°–70° W (Fig. 8.3a). The density of collected specimens was highest in northwestern Patagonia, the southern portion of Río Negro Province, and the central-northeastern strip of Chubut Province (Fig. 8.3b). The independence between high values of sampled localities vs. number of specimens collected for

Table 8.1 Lizards' presence recorded by vegetation units in Patagonia

Family	Genus	Species	Vegetation unit
Amphisbaenidae	*Amphisbaena*	*kingii*	MAT
		plumbea	DGSJ, DO, ER, MAT, MODT
Leiosauridae	*Diplolaemus*	*bibronii*	DC, DCE, DCEAS, DGSJ, DO, DSECB
		darwinii	DC, DCE, DGSJ, DO, EAMN, EP
		leopardinus	DLP, PA
		sexcinctus	BC, BAP, DCEAQ, DCEAS, DLP, DO, DSECB, ER, PA
	Leiosaurus	*bellii*	DCE, DCEAQ, DCEAS, DLP, DGSJ, DO, EPV, ER, MAT, MODT
	Pristidactylus	*araucanus*	DLP, DO, PA
		fasciatus	MAT, MODT
		nigroiugulus	DCE, DCEAQ, DCEAS, DO, MAT
		torquatus	BC, BEsc, BEsp, BL, BR
Liolaemidae	*Liolaemus*	*abdalai*	BAP, DSECB, PA
		antumalguen	DLP, MAT, PA
		araucaniensis	BC, BAP, DSECB, PA
		archeforus	DC, DCE, DO, DSECB, DSEMS, EAMN, MC
		austromendocinus	DLP, DO, MAT, PA
		avilae	DSECB
		baguali	DC, DCE
		bibronii	BAP, DC, DCE, DCEAQ, DCEAS, DLP, DGSJ, DO, DSECB, ER, EP, MAT, PA
		boulengeri	DCE, DCEAQ, DCEAS, DGSJ, DO, DSECB
		brattstroemi	BS
		buergeri	BC, BR, DO, DSECB, HA, MBA, MAT, PA
		burmeisteri	DLP
		calliston	MAT
		camarones	DGSJ
		canqueli	DCE, DCEAQ, DCEAS, DO
		caparensis	DCE
		carlosgarini	BC, MBA
		casamiquelai	DCEAQ, DO
		ceii	BAP, DSECB, PA
		chacabucoense	DC, EP
		chehuachekenk	DCEAQ, DO
		chiliensis	BC, BEsc, BEsp, BL, BR, BAP, DSECB, MBA, PA
		chillanensis	BC
		choique	PA
		coeruleus	DSECB, MBA, PA

(continued)

Table 8.1 (continued)

Family	Genus	Species	Vegetation unit
		confusus	BEsc
		crandalli	DLP
		cristiani	BC
		curicensis	BC, MBA
		curis	MBA
		cuyanus	MAT
		cuyumhue	MAT
		cyaneinotatus	DLP
		cyanogaster	BC, BEsc, BL, BR, BS, DSECB, PA
		darwinii	BEnd, DCEAQ, DLP, DO, EPV, ER, MAT, MODT, PA
		donosobarrosi	MAT
		duellmani	PA
		dumerili	ER, MAT
		elongatus	BAP, DCE, DCEAQ, DCEAS, DLP, DO, DSECB, ER, MAT, PA
		escarchadosi	DCE, DSECB, DSEMS, EAMN, SV
		exploratorum	DO
		fitzingerii	DC, DCE, DCEAQ, DCEAS, DGSJ, DO, DSECB, MAT
		flavipiceus	MBA, PA
		gallardoi	DC, DCE, DO
		goetschi	DO, ER, MAT
		gracilis	DCEAQ, DLP, DO, EPV, ER, MAT, MODT, PA
		gravenhorstii	BC, BEsc, BL
		grosseorum	DLP, ER, MAT
		gununakuna	DO, MAT
		hatcheri	BAP, DC, DCE
		hermannunezi	BC
		inacayali	DCEAQ, DO, ER
		janequeoae	BC
		josei	DLP, MAT, PA
		kingii	DC, DCE, DCEAS, DGSJ, DO, DSECB, DSEMS, EAMN, EP, PA
		kolengh	DSECB, EP, HA, SV
		kriegi	BC, BAP, DCEAQ, DO, DSECB
		leftrarui	BC
		lemniscatus	BC, BEsc, BL, BR, BAP, MBA, PA
		lentus	MAT
		lineomaculatus	BAP, DC, DCE, DO, DSECB, EAMN, MC, PA
		loboi	BAP, DCEAQ, DO, DSECB

(continued)

Table 8.1 (continued)

Family	Genus	Species	Vegetation unit
		magellanicus	BS, DFEMH, DSECB, DSEMS, EAMN, EP, MC
		mapuche	DLP, DO, MAT
		martorii	MAT, MODT
		melanops	DCE, DCEAQ, DO, EPV, ER, MAT
		monticola	BC, BR
		morandae	DGSJ, DO
		morenoi	DLP, DO
		multimaculatus	MAT, MODT
		neuquensis	DSECB, PA
		nitidus	BEsc, BEsp
		parthenos	DLP, MAT
		petrophilus	DCE, DCEAQ, DCEAS, DO, ER, MAT
		pictus	BC, BEsc, BEsp, BL, BR, BS, BAP, DSECB, MBA, PA, SV
		puelche	PA
		punmahuida	MAT, PA
		purul	BAP, DO
		rabinoi	MAT
		riodamas	MBA
		rothi	BAP, DCEAQ, DO, DSECB, ER, MAT
		sagei	DO
		sarmientoi	DSEMS
		schroederi	BC, BEsc, BEsp, BL, BR, MBA
		scolaroi	DSECB, EP, HA, MC, SV
		scorialis	BC, BR
		senguer	DCE, DCEAS, DGSJ, DO
		septentrionalis	BC, BR
		shehuen	DCEAQ, DO, MAT
		shitan	ER
		silvanae	DSECB
		sitesi	DLP
		smaug	PA
		somuncurae	DCEAQ, DO
		tari	DCE
		tehuelche	DO
		telsen	DO
		tenuis	BC, BEsc, BEsp, BL, BR, BAP, DSECB, MBA, PA
		thermarum	PA
		tirantii	DO, MAT
		tregenzai	BC, PA

(continued)

Table 8.1 (continued)

Family	Genus	Species	Vegetation unit
		tristis	DCE, DO
		tromen	DO, DSECB, MAT, PA
		uptoni	DO
		villaricensis	SV
		wiegmannii	MAT, MODT
		xanthoviridis	DCE, DCEAQ, DGSJ, MAT
		yatel	DCE
		zabalai	BC, MBA
		zullyae	DCE, DSECB, EP, HA, MC
	Phymaturus	*cacivioi*	DO
		calcogaster	DCEAQ, MAT
		camilae	DO
		castillensis	DCE
		ceii	DCEAQ, DO, ER, MAT
		curivilcun	DO
		delheyi	PA
		desuetus	DCEAQ
		dorsimaculatus	DSECB, PA
		etheridgei	DCEAQ, DO
		excelsus	DO
		felixi	DCEAS
		indistinctus	DCE, DCEAS, DO
		manuelae	DCEAQ
		maulense	BC, MBA
		nevadoi	DLP
		palluma	PA
		patagonicus	MAT
		payuniae	DLP
		querque	DO
		rahuensis	DSECB
		roigorum	DLP
		sinervoi	DO
		sitesi	DLP
		somuncurensis	DCEAQ, DO, ER
		spectabilis	DCEAQ
		spurcus	DCEAQ, DO
		tenebrosus	DO, DSECB
		tromen	PA
		verdugo	PA
		videlai	DCEAS
		vociferator	BC, PA
		yachanana	ER, MAT

(continued)

Table 8.1 (continued)

Family	Genus	Species	Vegetation unit
		zapalensis	DO
Phyllodactylidae	*Homonota*	*darwinii*	DCE, DCEAQ, DCEAS, DLP, DGSJ, DO, DSECB, EPV, ER, MAT, MODT, PA
		horrida	DLP, MAT
		underwoodi	MAT
Teiidae	*Aurivela*	*longicauda*	BEnd, DLP, DO, ER, MAT, PA
	Salvator	*rufescens*	MAT
	Teius	*oculatus*	BEnd, MAT, MODT
		teyou	MAT
Tropiduridae	*Stenocercus*	*pectinatus*	MAT, MODT

References: Endorheic Bolsons = BEnd, Deciduous Forest = BC, Sclerophyllous Forest = BEsc, Thorny Forest = BEsp, Laurel Forest = BL, Resinous Forest = BR, Evergreen Forest = BS, Andean—Patagonian Forests = BAP, Central District = DC, Erial Central District = DCE, Central District—Quilenbai steppe bushes = DCEAQ, Central District—Mountain steppe bushes = DCEAS, Payunia District = DLP, San Jorge Gulf District = DGSJ, Fueguino District—Wet Magellanic Steppe = DFEMH, Western District = DO, Sub Andean District—Steppe of white coiron = DSECB, Sub Andean District—Dry magellanic steppe = DSEMS, Valdés Península Ecotone = EPV, Rionegrino Ecotone = ER, Shrub steppe of black bush = EAMN, Steppes and pastures = EP, Altitude grass = HA, Low altitude scrub = MBA, Deciduous scrub = MC, Evergreen shrub = MS, Typical southern Monte = MAT, Monte's Mountains and Valleys = MSB, Eastern or Transitional Monte = MODT, Western Interior Pampa = PIO, Altoandina Province = PA, Peat Bogs = T, and Without vegetation = SV

some cells indicates no absolute positive relationship between these two variables. Species richness was highest in northern Patagonia, west of Río Negro Province, the northeast and southeast strip of Chubut Province, and north of Santa Cruz Province (Fig. 8.3c).

Species richness gradually increased from 34° to 36° S and peaked between 37°–39° S at 49 species, and then gradually decreased toward the south (Fig. 8.4a). This pattern was clearly not correlated with the number of records, which indicated a homogeneous sampling with only a small increase in around 42° S (Fig. 8.4c). The analysis based on longitude showed that on both marine coasts (Pacific and Atlantic) there are very few locality records as well as in the Andean zone between 72° and 73° W, while the largest amount was located between 72°–65° W (Fig. 8.4d). Longitudinally, species richness showed a clear relationship with the number of records. We found the greatest species richness between 71° and 69° W, with a maximum of 75 species (Fig. 8.4b).

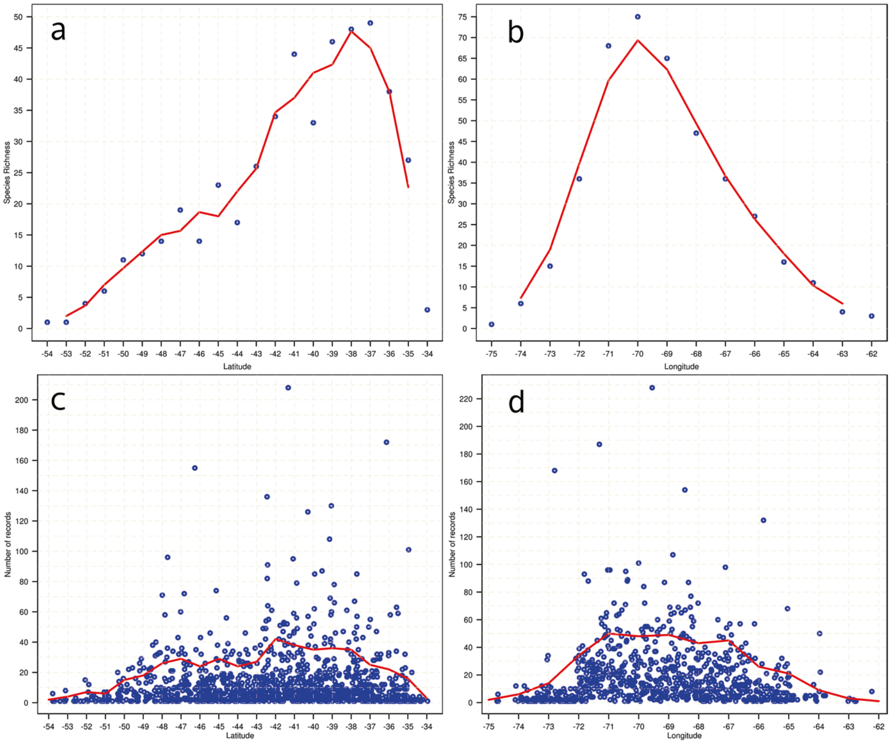


Fig. 8.4 Cumulative spatial analysis of Patagonian lizards. References: red lines (implementing movingFun function with “moving average” from R “raster” package); (**a**) number of accumulated species by latitude; (**b**) number of accumulated species by longitude; (**c**) number of accumulated records by latitude; (**d**) number of accumulated records by longitude

8.5 Ecological Aspects of Lizards in Patagonia’s Ecoregions

Several studies found a relationship between lizards’ ecology, such as feeding (Celedón-Neghme et al. 2005; Corbalán and Debandi 2014), shelter (Halloy et al. 2013) and thermoregulation (Ibargüengoytía 2005; Cruz et al. 2009), and vegetation of the environments they inhabit. The combination of these aspects that are directly influenced by vegetation type might determine the presence of lizard species (Pietrek et al. 2009; Halloy et al. 2013). Hence, we decided to assess the relationship between vegetation units and lizard richness in Patagonia.

We found lizards in 29 of the 33 vegetation units. We found no lizard records in Evergreen shrub, Monte’s Mountains and Valleys, Western Interior Pampa, and Peat Bogs (Fig. 8.5). The units with the highest species richness (*S*) in northern and central Argentinean Patagonia, reaching western Chubut Province were the Western District (60) and Typical southern Monte (49), followed in *S* by Altoandina Province (40) that is restricted to Andean environments. We found low *S* values in northern Chilean Patagonia, pre-mountain range and south of Santa Cruz Province in

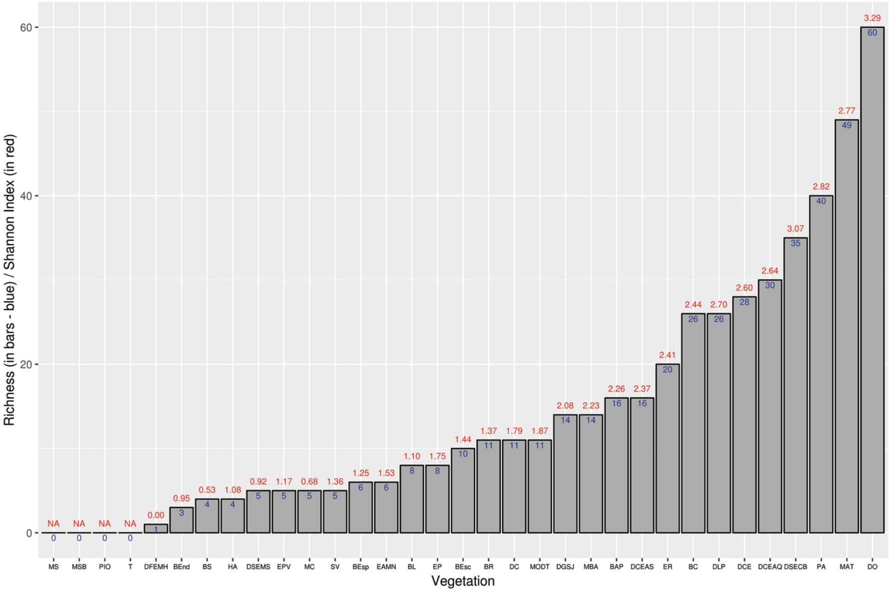


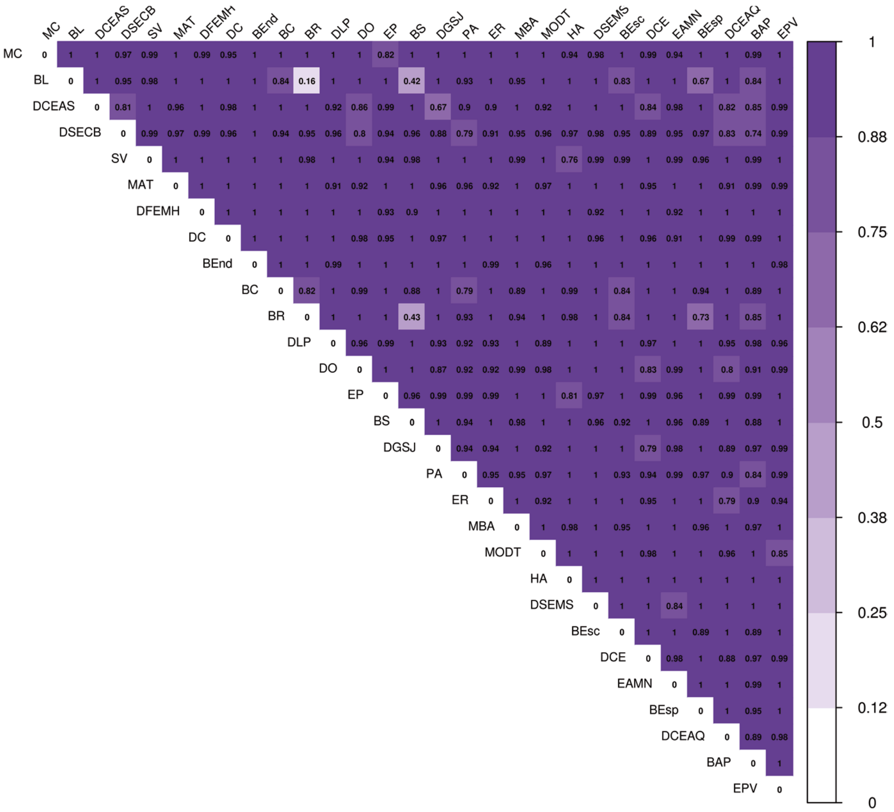
Fig. 8.5 Bar plot with lizard species richness in increasing order for each vegetation unit. References: number of species in blue, Shannon Wiener Index in red; Endorheic Bolsons = BEnd, Deciduous Forest = BC, Sclerophyllous Forest = BEsc, Thorny Forest = BEsp, Laurel Forest = BL, Resinous Forest = BR, Evergreen Forest = BS, Andean—Patagonian Forests = BAP, Central District = DC, Erial Central District = DCE, Central District—Quilenbai steppe bushes = DCEAQ, Central District—Mountain steppe bushes = DCEAS, Payunia District = DLP, San Jorge Gulf District = DGSJ, Fueguino District—Wet Magellanic Steppe = DFEMH, Western District = DO, Sub Andean District—Steppe of white coiron = DSECB, Sub Andean District—Dry Magellanic Steppe = DSEMS, Valdés Península Ecotone = EPV, Rionegrino Ecotone = ER, Shrub steppe of black bush = EAMN, Steppes and pastures = EP, Altitude grass = HA, Low altitude scrub = MBA, Deciduous scrub = MC, Evergreen shrub = MS, Typical southern Monte = MAT, Monte's Mountains and Valleys = MSB, Eastern or Transitional Monte = MODT, Western Interior Pampa = PIO, Altoandina Province = PA, Peat Bogs = T, and Without vegetation = SV

Argentina: Sub Andean District—Steppe of white coiron (35), Central District—Quilenbai steppe bushes (30), Erial Central District (28), Deciduous Forest (26), and Payunia District (26). Without a clear spatial pattern, we found an even lower *S* for the Rionegrino Ecotone (20), Andean—Patagonian Forests and Central District—Mountain steppe bushes (16), and San Jorge Gulf District and Low altitude scrub (14). We found the lowest *S* values in northern Chile (Resinous Forest: 11, Sclerophyllous Forest: 10, Thorny Forest: 6, Laurel Forest: 8, and Altitude grass: 4) and in vegetation units located south of 41° S (Deciduous scrub and Without vegetation: 5, and Evergreen Forest: 4). Finally, we recorded the lowest *S* values for Argentina in the northern and eastern strip (Eastern or Transitional Monte: 11, Valdés Península Ecotone: 5 and Endorheic Bolsons: 3) and in the southern strip of Patagonia (Central District: 11, Shrub steppe of black bush: 6, Sub Andean District—Dry Magellanic Steppe: 5 and Fueguino District—Wet Magellanic

Steppe: 1). The vegetation units and their species richness are detailed in Fig. 8.1b, c, and vegetation units by species in Table 8.1.

The Shannon Wiener diversity index (*H*) is one of the most commonly indices used to characterize species diversity in a community and accounts for both abundance and evenness (E_H) of the species present (*S*) (Colwell 2009). Technically, *H* quantifies the uncertainty associated with predicting the identity of taxa given the number of taxa and evenness in abundances of individuals within each taxon (Gotelli and Colwell 2001; Chao and Chiu 2016). The *S* values of the vegetation units varied from 0 to 60 species and the average *H* indices among the 29 vegetation types ranged from 0 to 3.29. Vegetation units with moderate *S* values between 1 and 8 (DFEMH, BEnd, BS, HA, DSEMS, EPV, MC, SV, BEsp, EAMN, BL, EP) showed a gradual *H* increase. DFEMH unit showed only *Liolaemus magellanicus* presence and BEnd was represented mostly by *L. darwinii*. BS and HA had the same number of species, but the E_h of BS is lower and is mostly represented by *L. pictus,* whereas HA is mainly formed by *L. kolengh*. The units DSEMS, EPV, MC, and SV had five species, but showed different E_H. In DSEMS we found *L. sarmientoi* as the most frequent species, EPV and SV had a more equitable distribution of the species that conform them, and MC is mostly represented by *L. scolaroi*. The vegetation units BEsp and EAMN had six species with equality components, while BL and EP had eight species, but BL was mostly represented by *L. pictus*. We found a greater frequency of *L. lemniscatus* presence for BEsc, *L. pictus* for BR, *L. baguali* and *L. hatcheri* for DC, *Homonota darwinii* for MODT, *L. fitzingerii* and *L. kingii* for DGSJ, *L. curis* for MBA, and *L. elongatus* for BAP. DCEAS and ER units showed greater evenness among the taxa present there without a dominant species. The species *L. pictus* and *L. tenius* showed high frequency for BC, *L. austromendocinus* for DLP, *L. kingii* for DCE, *L. inacayali* for DCEAQ, *L. pictus* for PA, and *L. darwinii* for MAT. Finally, DO and DSECB showed high evenness (Fig. 8.5).

The Jaccard similarity index (Chao et al. 2005) compares members of two datasets to see which members are shared and which are distinct, and ranges from 0 to 1 (1 = no taxon in common; 0 = all taxa in common). It is usually implemented at large spatial scales (e.g., comparing regions) to assess biodiversity considering only species' presence-absence records (Real et al. 1996). According to these similarity comparisons, none of the 406 paired comparisons among vegetation units had the exact same taxa (Fig. 8.6). Most of the paired comparisons (217) had values of 1, indicating that in most cases vegetation units do not have any lizard species in common (Fig. 8.6). By contrast, 189 comparisons had values less than one (Fig. 8.6) and the greatest similarity was found between BL versus BR (0.16), BS (0.42) and BEsp (0.67), BR versus BS (0.43); and DGSJ versus DCEAS (0.67).



	MC	BL	DCEAS	DSECB	SV	MAT	DFEMH	DC	BEnd	BC	BR	DLP	DO	EP	BS	DGSJ	PA	ER	MBA	MODT	HA	DSEMS	BEsc	DCE	EAMN	BEsp	DCEAQ	BAP	EPV
MC	0	1	1	0.97	0.99	1	0.99	0.95	1	1	1	1	1	0.82	1	1	1	1	1	1	0.94	0.98	1	0.99	0.94	1	1	0.99	1
BL		0	1	0.95	0.98	1	1	1	1	0.84	0.16	1	1	1	0.42	1	0.93	1	0.95	1	1	1	0.83	1	1	0.67	1	0.84	1
DCEAS			0	0.81	1	0.96	1	0.98	1	1	1	0.92	0.86	0.99	1	0.67	0.9	0.9	1	0.92	1	1	1	0.84	0.98	1	0.82	0.85	0.99
DSECB				0	0.99	0.97	0.99	0.96	1	0.94	0.95	0.96	0.8	0.94	0.96	0.88	0.79	0.91	0.95	0.96	0.97	0.98	0.95	0.89	0.95	0.97	0.83	0.74	0.99
SV					0	1	1	1	1	1	0.98	1	1	0.94	0.98	1	1	1	0.99	1	0.76	0.99	0.99	1	0.99	0.96	1	0.99	1
MAT						0	1	1	1	1	1	0.91	0.92	1	1	0.96	0.96	0.92	1	0.97	1	1	1	0.95	1	1	0.91	0.99	0.99
DFEMH							0	1	1	1	1	1	1	0.93	0.9	1	1	1	1	1	1	0.92	1	1	0.92	1	1	1	1
DC								0	1	1	1	1	0.98	0.95	1	0.97	1	1	1	1	1	0.96	1	0.96	0.91	1	0.99	0.99	1
BEnd									0	1	1	0.99	1	1	1	1	1	0.99	1	0.96	1	1	1	1	1	1	1	1	0.98
BC										0	0.82	1	0.99	1	0.88	1	0.79	1	0.89	1	0.99	1	0.84	1	1	0.94	1	0.89	1
BR											0	1	1	1	0.43	1	0.93	1	0.94	1	0.98	1	0.84	1	1	0.73	1	0.85	1
DLP												0	0.96	0.99	1	0.93	0.92	0.93	1	0.89	1	1	1	0.97	1	1	0.95	0.98	0.96
DO													0	1	1	0.87	0.92	0.92	0.99	0.98	1	1	1	0.83	0.99	1	0.8	0.91	0.99
EP														0	0.96	0.99	0.99	0.99	1	1	0.81	0.97	1	0.99	0.96	1	0.99	0.99	1
BS															0	1	0.94	1	0.98	1	1	0.96	0.92	1	0.96	0.89	1	0.88	1
DGSJ																0	0.94	0.94	1	0.92	1	1	1	0.79	0.98	1	0.89	0.97	0.99
PA																	0	0.95	0.95	0.97	1	1	0.93	0.94	0.99	0.97	0.9	0.84	0.99
ER																		0	1	0.92	1	1	1	0.95	1	1	0.79	0.9	0.94
MBA																			0	1	0.98	1	0.95	1	1	0.96	1	0.97	1
MODT																				0	1	1	1	0.98	1	1	0.96	1	0.85
HA																					0	1	1	1	1	1	1	1	1
DSEMS																						0	1	1	0.84	1	1	1	1
BEsc																							0	1	1	0.89	1	0.89	1
DCE																								0	0.98	1	0.88	0.97	0.99
EAMN																									0	1	1	0.99	1
BEsp																										0	1	0.95	1
DCEAQ																											0	0.89	0.98
BAP																												0	1
EPV																													0

Fig. 8.6 Jaccard similarity index pairwise comparisons between species and vegetation units. References: 0 = identical species, 1 = different species, Endorheic Bolsons = BEnd, Deciduous Forest = BC, Sclerophyllous Forest = BEsc, Thorny Forest = BEsp, Laurel Forest = BL, Resinous Forest = BR, Evergreen Forest = BS, Andean—Patagonian Forests = BAP, Central District = DC, Erial Central District = DCE, Central District—Quilenbai steppe bushes = DCEAQ, Central District—Mountain steppe bushes = DCEAS, Payunia District = DLP, San Jorge Gulf District = DGSJ, Fueguino District—Wet Magellanic Steppe = DFEMH, Western District = DO, Sub Andean District—Steppe of white coiron = DSECB, Sub Andean District—Dry Magellanic Steppe = DSEMS, Valdés Península Ecotone = EPV, Rionegrino Ecotone = ER, Shrub steppe of black bush = EAMN, Steppes and pastures = EP, Altitude grass = HA, Low altitude scrub = MBA, Deciduous scrub = MC, Typical southern Monte = MAT, Eastern or Transitional Monte = MODT, Altoandina Province = PA, and Without vegetation = SV

8.6 Spatial Patterns for Patagonian Lizard Assemblages

Organism assemblages can provide a conceptual basis for understanding the processes that determine how many, which and how species that inhabit in a particular region relate (Chase 2003). Regional and local factors can determine the patterns by which communities of organisms are assembled, as well as the resulting degree of

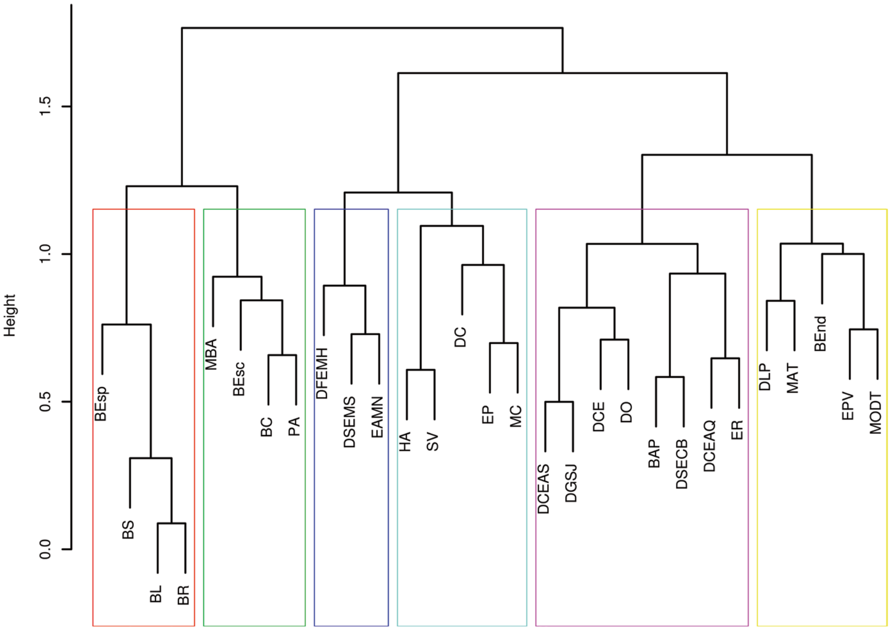


Fig. 8.7 Species hierarchic clustering using vegetation units as clusters. References: Endorheic Bolsons = BEnd, Deciduous Forest = BC, Sclerophyllous Forest = BEsc, Thorny Forest = BEsp, Laurel Forest = BL, Resinous Forest = BR, Evergreen Forest = BS, Andean—Patagonian Forests = BAP, Central District = DC, Erial Central District = DCE, Central District—Quilenbai steppe bushes = DCEAQ, Central District—Mountain steppe bushes = DCEAS, Payunia District = DLP, San Jorge Gulf District = DGSJ, Fueguino District—Wet Magellanic Steppe = DFEMH, Western District = DO, Sub Andean District—Steppe of white coiron = DSECB, Sub Andean District—Dry Magellanic Steppe = DSEMS, Valdés Península Ecotone = EPV, Rionegrino Ecotone = ER, Shrub steppe of black bush = EAMN, Steppes and pastures = EP, Altitude grass = HA, Low altitude scrub = MBA, Deciduous scrub = MC, Typical southern Monte = MAT, Eastern or Transitional Monte = MODT, Altoandina Province = PA, and Without vegetation = SV

similarity or difference between localities with similar environments (see Thompson et al. 2016; Palmeirim et al. 2017).

Hierarchical clustering is one of the most typical multivariate ordination and agglomerative analysis for biological communities (McGarigal et al. 2013). These methods start with combining two most similar sites to each other, then they proceed by combining points to points or to groups, or groups to groups using different aggregation criteria (Gardener 2014). We used the vegan R package (Oksanen et al. 2018) to implement a hierarchical clustering from the vegdist' similar -dissimilarity structure from the "hclust" function ("stats" R base package), which needs dissimilarities as input. Function "hclust" provides several alternative clustering strategies, and we selected the Ward's minimum variance method. This method minimizes the total within-cluster variance, merging at each step the pair of clusters with minimum between-cluster distance. We found six clusters of vegetation units (Fig. 8.7). All of these clusters had differences higher than one, and within the clusters there were differences in distance among their components. In the first cluster (in red), the most different unit of vegetation was BEsp, and the fourth cluster (cyan) showed differences between HA + SV versus DC, and EP + MP. The fifth cluster (magenta) showed differences between DCEAS + DGSJ + DCE + DO versus BAP + DSECB + DCEAQ + ER, and in the sixth group (yellow) showed differences for DLP + MAT versus BEnd + EPV + MODT (Fig. 8.7). To compare the diversity of species among the vegetation units, we considered the groups defined by this hierarchical clustering.

The species richness metric increases with sample size, and differences in richness actually may be caused by differences in sample size. To address this potential bias, we used rarefaction curves to rarefy species richness to the same number of individuals, because they are often seen as an objective solution for comparing species richness with different sample sizes. We implemented rarefaction curves and evaluated them using the interval of step sample sizes, determined by the minimum sample count achieved over each cluster. The number of expected species was between 2.42 and 4.25 for BEnd, EPV, MODT, and MAT at the same minimal subsample of 5. The number of expected species within clusters were BAP (15.88), DCEAS (15.88), DGSJ (13.56), ER (19.35), DSECB (33), DCEAQ (26.56), DCE (24.88), and DO (46.76) at the minimal subsample of 346. The number of expected species within clusters were SV (5), HA (3.80), MC (3.10), EP (5.72), and DC (6.30) at the minimal subsample of 19. The number of expected species within clusters was DFEMH (1), DSEMS (2.96), and EAMN (4.37) at the minimal subsample of 10. The number of expected species within clusters was MBA (14), BEsc (9.40), BC (23.34), and PA (29.80) at the minimal subsample of 205. The number of expected species within clusters was BEsp (6.00), BS (3.12), BL (5.55), and BR (7.50) at the minimal subsample of 34 (Fig. 8.8).

The parameters referring to landscape structure (e.g., altitude) are essential in any biogeography study given the relationship between landscape structure and the ecological processes (Jongman et al. 1995). In the altitude analysis, we found a higher limit between 2100 and 2400 m a.s.l. for the genera *Phymaturus*, *Pristidactylus*, *Diplolaemus*, *Liolaemus*, and *Homonota*. On the other hand, *Leiosaurus*, *Aurivela*, and *Amphisbaena* showed an upper limit of 1400 m a.s.l., while *Teius*, *Salvator*, and *Stenocercus* did not exceed 800 m a.s.l. (Fig. 8.9). Within the 34 *Phymaturus* taxa we found a group of species above 1450 m a.s.l.: *P. palluma*, *P. verdugo*, *P. roigorum*, *P. tromen*, *P. payuniae*, *P. maulense*, *P. dorsimaculatus*, *P. nevadoi*, *P. delheyi*, and *P. sitesi* up to a maximum of 2784 m a.s.l. We identified another group of species consisting of *P. vociferator*, *P. querque*, *P. zapalensis*, *P. somuncurensis*, *P. cacivioi*, *P. rahuensis*, *P. excelsus*, *P. desuetus*, *P. curivilcun*, *P. camilae*, *P. etheridgei*, *P. ceii*, *P. spurcus*, *P. tenebrosus*, *P. spectabilis*, and *P. sinervoi* between 865 and 1450 m a.s.l. Finally, we found *P. manuelae*, *P. videlai*, *P. calcogaster*, *P. yachanana*, *P. indistinctus*, *P. felixi*, *P. castillensis*, and *P. patagonicus* between 33 and 865 m a.s.l. (Fig. 8.10). Among the 110 *Liolaemus* taxa we found a group of species above 2365 m a.s.l.: *L. punmahuida*, *L. villaricensis*, *L. riodamas*, *L. thermarum*, and *L. antumalguen* up to a maximum height of 3000 m a.s.l. Another group with a narrow range of altitude was formed by *L.*

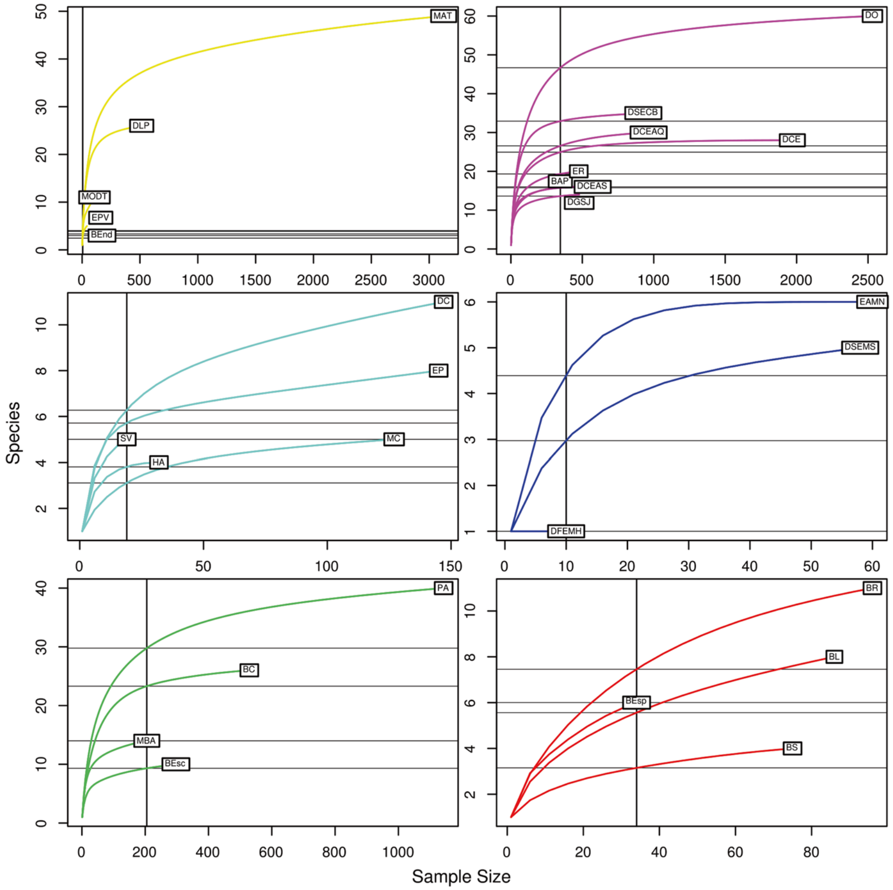


Fig. 8.8 Rarefy curves with the expected species richness in random subsamples of size sample among each cluster. Vertical line is drawn at minimum sample and horizontal lines for the rarefied species richnesses. References: Endorheic Bolsons = BEnd, Deciduous Forest = BC, Sclerophyllous Forest = BEsc, Thorny Forest = BEsp, Laurel Forest = BL, Resinous Forest = BR, Evergreen Forest = BS, Andean—Patagonian Forests = BAP, Central District = DC, Erial Central District = DCE, Central District—Quilenbai steppe bushes = DCEAQ, Central District—Mountain steppe bushes = DCEAS, Payunia District = DLP, San Jorge Gulf District = DGSJ, Fueguino District—Wet Magellanic Steppe = DFEMH, Western District = DO, Sub Andean District—Steppe of white coiron = DSECB, Sub Andean District—Dry Magellanic Steppe = DSEMS, Valdés Península Ecotone = EPV, Rionegrino Ecotone = ER, Shrub steppe of black bush = EAMN, Steppes and pastures = EP, Altitude grass = HA, Low altitude scrub = MBA, Deciduous scrub = MC, Typical southern Monte = MAT, Eastern or Transitional Monte = MODT, Altoandina Province = PA, and Without vegetation = SV

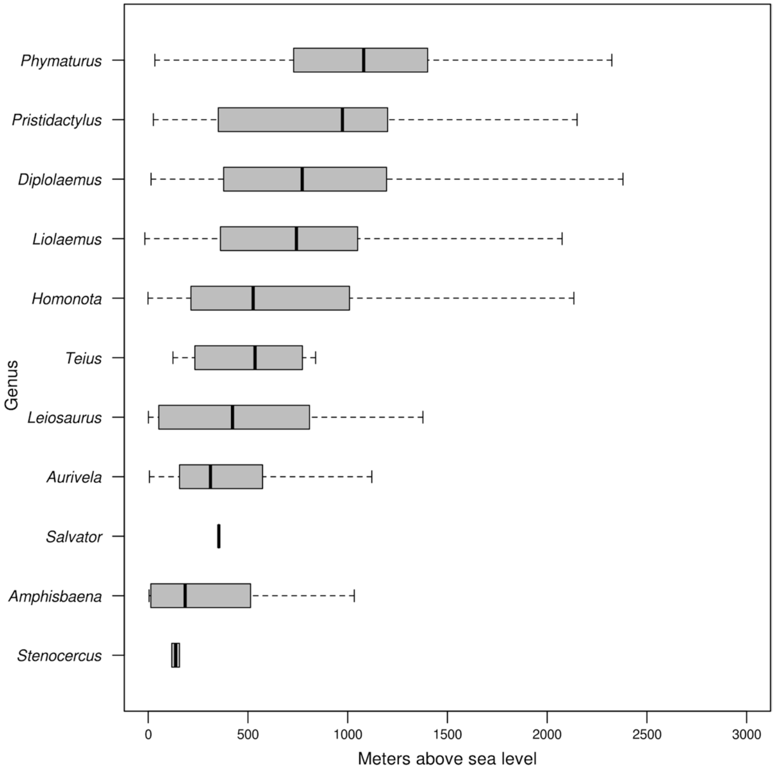


Fig. 8.9 Box plot of altitudinal range among lizards' genera in Patagonia

wiegmanni, *L. yatel*, *L. brattstroemi*, *L. camarones*, *L. martorii*, and *L. multimaculatus* between 0 and 64 m a.s.l. The rest of the *Liolaemus* taxa presented broader ranges or appeared to have restricted ranges, but those last ones actually had only few of geographical locations (Fig. 8.11).

8.7 Conclusions

The analyses performed for this chapter allowed us to transform an extensive review into synthetic results about the biogeography and species diversity of lizards in the vast Patagonian region. The increasing number of field samples, and the subsequent descriptions of new species during the last decades, considerably improved our understanding and knowledge of lizard species' distributions in the extreme south of South America. The geographic distribution data presented here should be permanently updated and subject to revisions by specialists in taxonomy, systematics,

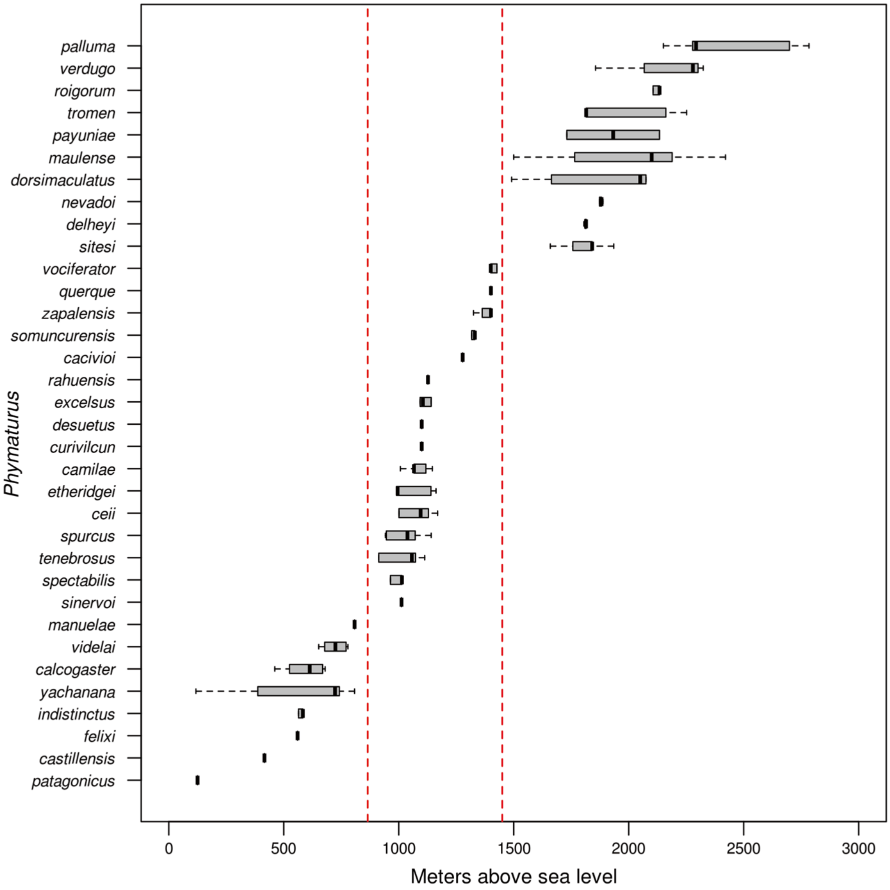


Fig. 8.10 Box plot of altitudinal range among *Phymaturus* species in Patagonia

and phylogeography, since there are numerous active research programs, which during the last 15 years have described, revalidated, and synonymized species as well as their distributions (mostly within *Liolaemus* and *Phymaturus* genera) (Avila et al. 2008; Abdala et al. 2012a, b; Vera-Escalona et al. 2012; Olave et al. 2014, 2015; Lobo et al. 2016; Troncoso-Palacios et al. 2016, 2018). To sum up, our spatial analyses improve our understanding of geographic distributions in one of the regions with

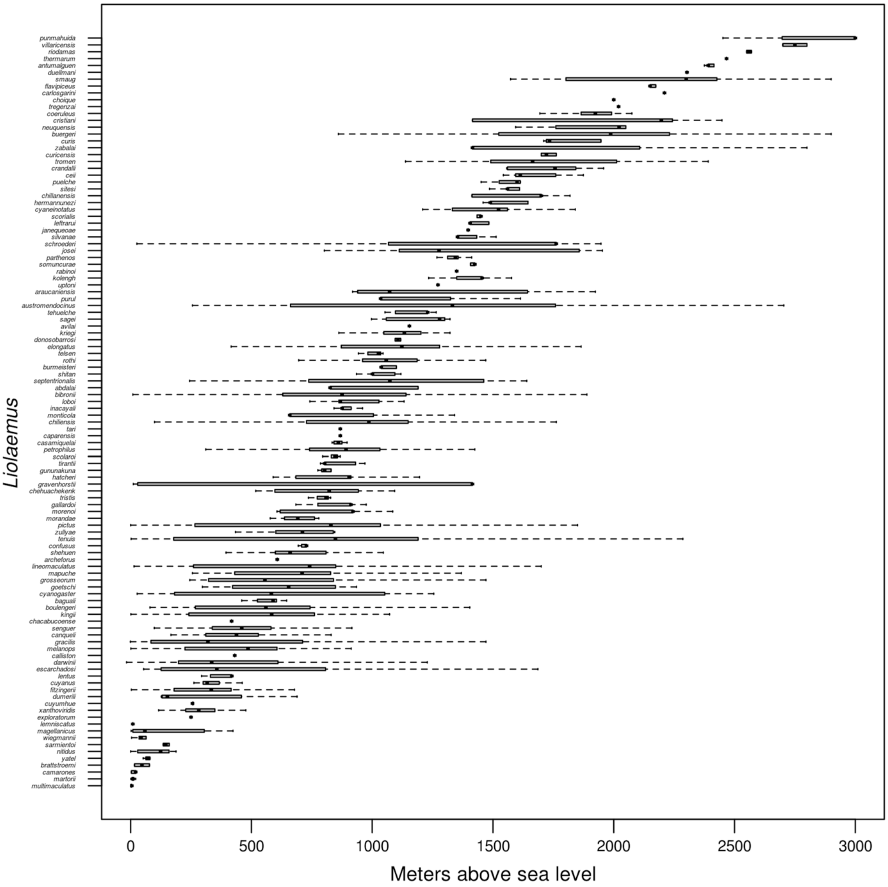


Fig. 8.11 Box plot of altitudinal range among *Liolaemus* species in Patagonia

the greatest diversity of lizards in the world and we provide ecological and spatial metrics with an updated list of taxa for Patagonian lizards. We highlight that the framework implemented here allows the analysis of large volumes of information and geographic space to obtain quantitative results that can support the study of spatial patterns of biodiversity, decision-making to design studies, use of resources, and creation of protected areas.

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Chapter 9

Diversification and Evolutionary Histories of Patagonian Steppe Lizards

Mariana Morando, Cintia Débora Medina, Ignacio Minoli, Cristian Hernán Fulvio Pérez, Jack W. Sites Jr, and Luciano J. Avila

Abstract During the last two decades, regional exploration coupled with dense geographic sampling, new molecular techniques, and phylogeographic approaches have led to the discovery of unexpected hidden diversity. These data have expanded inferences about evolutionary and demographic processes to explain patterns of geographic genetic distribution, phylogenetic history, and morphological characteristics. This chapter summarizes current knowledge of species boundaries and possible underlying processes, highlighting the extent of hybridization and its possible role for the lack of strongly supported phylogenetic relationships within several species groups.

Keywords Phylogeography · Phylogeny · Hybridization · Patagonia · Hidden diversity

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M. Morando (✉) · I. Minoli · L. J. Avila
Instituto Patagónico para el Estudio de los Ecosistemas Continentales – Consejo Nacional de Investigaciones Científicas y Técnicas (IPEEC-CONICET),
Puerto Madryn, Chubut, Argentina
e-mail: morando@cenpat-conicet.gob.ar; minolicnp@gmail.com;
avila@cenpat-conicet.gob.ar

C. D. Medina
Laboratorio de Genética Molecular – UAT, CCT-CONICET CENPAT,
Puerto Madryn, Chubut, Argentina
e-mail: medina@cenpat-conicet.gob.ar

C. H. F. Pérez
UAT, CCT-CONICET CENPAT, Puerto Madryn, Chubut, Argentina
e-mail: chfperez@cenpat-conicet.gob.ar

J. W. Sites Jr
Biology Department and Monte L. Bean Life Science Museum, Brigham Young University,
Provo, UT, USA

Department of Biology, Austin Peay State University, Clarksville, TN, USA
e-mail: jwsites6098@gmail.com

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9.1 Lizard Clades in Patagonia: A Starting Point for Phylogeography and Phylogeny

Phylogeography was born as and still is a bridge, in geography and time, between population biology and phylogenetics (Avise et al. 1987; Edwards et al. 2016). A brief summary of the characteristics and evolution of phylogeography as a distinct discipline, particularly in relation to Patagonian lizards, is detailed in Chap. 10. Its central position and linkage between the disciplines of population genetics and phylogenetics is clearly reflected in the reciprocal illumination between phylogenetic and phylogeographic studies performed on multiple lizard clades from the Patagonian steppe, which we summarize in this chapter. A review of taxonomic histories is beyond the scope of this work (for a review of the taxonomic history of *Liolaemus* see Chap. 7; Abdala 2007; for *Phymaturus* Lobo et al. 2016, 2018; for *Homonota* Morando et al. 2014; and for Morando et al. 2020; Femenías et al. 2020). In this chapter, we briefly summarize most of the recent phylogeographic studies of Patagonian Steppe lizards, the current state of knowledge based on strongly supported hypothesis of species boundaries and evolutionary relationships, and consider some future directions for further research.

The majority of Patagonian lizard species are part of the Iguanian rank free clade Liolaemini (sensu Schulte II et al. 2003; = family Liolaemidae); three genera are recognized, two of which are widely distributed in this area: the extremely diverse *Liolaemus* and its sister genus *Phymaturus*, while the monotypic *Ctenoblepharys* is distributed in Perú. The first comprehensive mitochondrial (hereafter mtDNA) phylogenetic hypothesis for *Liolaemus* was published in 2000 (Schulte II et al. 2003), and included 60 species, of which 14 are distributed in Patagonian steppe and three in the western Andean area. This tree supported two main clades (previously proposed by Laurent 1983), *Liolaemus* sensu stricto and *Eulaemus* (some authors refer to these as subgenera), and nested within *Eulaemus* the two clades *L. lineomaculatus* and *L. montanus* sections. This same topology was supported in later studies based on new mitochondrial and nuclear gene regions (Morando 2004; Espinoza et al. 2004; Pincheira-Donoso et al. 2013; Olave et al. 2014, 2015; Esquerré et al. 2019a), and constitutes a strongly supported and well-resolved hypothesis.

Although in Patagonia we find representatives of all these clades, the *L. lineomaculatus* section and other species groups/complexes within *Eulaemus* (*L. fitzingerii*, *L. boulengeri*) are confined exclusively to Patagonia, while others have only their southernmost distributions in the region (*L. darwinii*, *L. wiegmannii*, *L. duellmani* from *L. montanus* group). A few clades within the large *Liolaemus* sensu stricto clade also have almost exclusive Patagonian Steppe distributions (*L. elongatus*, *L. kriegi*, and *L. bibronii* complexes). The sister genus *Phymaturus* includes 48 species, which are also resolved into two strongly supported main clades (Etheridge 1995; Espinoza et al. 2004; Lobo and Quinteros 2005a, b; Morando et al. 2013; Esquerré et al. 2019a; Olave et al. 2020b). A northern *P. palluma* clade includes species with distributions extending into northwestern Patagonia, whereas the *P. patagonicus* clade is strictly distributed in the Patagonian

Steppe. The southernmost distributions of some of the *P. palluma* clades overlap with the northernmost species of the *P. patagonicus* clade. Given the high diversity of the clade Liolaemini, particularly the genus *Liolaemus*, the majority of earlier phylogenetic papers sampled species broadly from different clades, but with less dense sampling of species within clades. Furthermore, some authors have focused on higher taxonomic level "general squamate" studies (e.g., Wiens et al. 2012; Pyron et al. 2013), and have included all available data in GenBank at that time, to generate supertrees. These more inclusive studies are of limited value here, and we consider specific detailed studies of Patagonian species only.

The second Iguanian clade, primarily endemic to Patagonia is Leiosaurae. This clade includes three genera: (1) *Leiosaurus*, of which *L. bellii* is widely distributed in northern and northwestern Patagonia, while the other three species have more restricted distributions north of Patagonia; (2) *Diplolaemus*, with four Patagonian species, *D. darwinii*, *D. bibronii*, *D. sexcinctus*, *D. leopardinus;* three of these are widely distributed across the Patagonian Steppe, and the fourth is more restricted to northwestern Patagonia; and (3) *Pristidactylus*, four of its ten species (*P. nigroiugulus*, *P. araucaniensis*, *P. fasciatus*, and *P. scapulatus*) are Patagonian. Morando et al. (2020) used two mitochondrial and eight nuclear gene regions to infer phylogenetic relationships for individuals from type localities for almost all species of Leiosaurae. The origin of this clade was estimated at ~18 Ma with the oldest divergences within *Diplolaemus* and *Leiosaurus* respectively (~15–9 Ma), and several more recent divergences within the three genera. The only species distributed in the coastal cordillera of Nahuelbuta in Chile (*P. torquatus*) was inferred as an old divergence within Leiosaurae (~15 Ma), and as a separate lineage from the rest of *Pristidactylus* species distributed in the Andes and in Argentina, suggesting it may represent a different genus. The first phylogeographic study for most of the Patagonian species of Leiosaurae has been published during the printing of this book (Femenías et al. 2020).

The Gekkota clade in Patagonia is represented by three species of the genus *Homonota* (which currently includes 12 species): *H. darwinii* is widely distributed across the Steppe, whereas *H. horrida* and *H. underwoodi* are confined to the Monte region of northern Patagonia. These results are based on a recently published multilocus (two mtDNA and nine nuclear genes) phylogenetic hypothesis (Morando et al. 2014), and an integrative phylogeographic study of *H. darwinii* and *H. horrida* is currently underway (Morando, unpublished).

The Lacertoidea (Teiidae) is marginally represented in northern Patagonia with the southernmost part of the distribution of *Aurivela longicauda.* This taxon was included in an mtDNA-based phylogeographic study that showed its presence in this area is most probably the result of recent range expansion (Yoke et al. 2006).

9.2 Hidden Diversity

The first phylogeographic studies in the early 2000s focused on Patagonian lizards initiated a new era of discovery (Morando et al. 2003, 2004, 2007; Avila et al. 2006). These studies were based on "mtDNA gene trees", focused on more intense geographic and individual sampling of widely distributed *Liolaemus* species in the Patagonian steppe. The first study (Morando et al. 2003) focused on three species complexes (*L. elongatus*, *L. kriegi*, *L. petrophilus*) that at the time included 11 recognized species, but the mtDNA tree resolved 12 unexpected, well-supported, geographically concordant, haploclades; all were referred to as "candidate species" deserving further integrative studies. The majority of these have now been formally described as new species. At that time the genus included 146 described species, but results of this first study led to extrapolations for other *Liolaemus* clades, and suggested that the genus may include more than 320 species. The genus now includes 261 described species, and subsequent densely sampled phylogeographic studies on other groups (Morando et al. 2004, 2007; Avila et al. 2006) have revealed more hidden diversity and new hypotheses of candidate species. Also, Abdala (2007) inferred a parsimony total evidence tree based on 128 morphological characters (32 morphometric) and 1776 bp of mtDNA for 67 taxa representatives of the *L. boulengeri* series included in the *Eulaemus* clade (subgenus), and 16 of them were hypothesized as candidate species. More recent studies have compared the level of morphological and molecular divergence in *Liolaemus boulengeri* and *rothi* species complexes (Olave et al. 2018) and *Phymaturus patagonicus* (Marín et al. 2018), demonstrating a mismatch of little morphological differentiation compared to the deep molecular divergence.

Table 9.1 summarizes the number of individuals and localities sampled for all phylogeographic studies published for Argentinean Patagonian *Liolaemus*. A similar first comprehensive molecular study of phylogenetic relationships for 32 of the 38 described species at that time of the sister genus *Phymaturus* (Morando et al. 2013), based on 2 mitochondrial and 11 nuclear gene sequences resolved a remarkable 22 candidate species. Some relationships in this study did not have strong support, leaving open the possibility that more dense geographic sampling and inclusion of additional gene regions will likely identify additional candidate species. Subsequent studies including morphological data, the addition of new sequences,

Table 9.1 Number of localities and individuals sampled for phylogeographic studies of Patagonian *Liolaemus* lizards

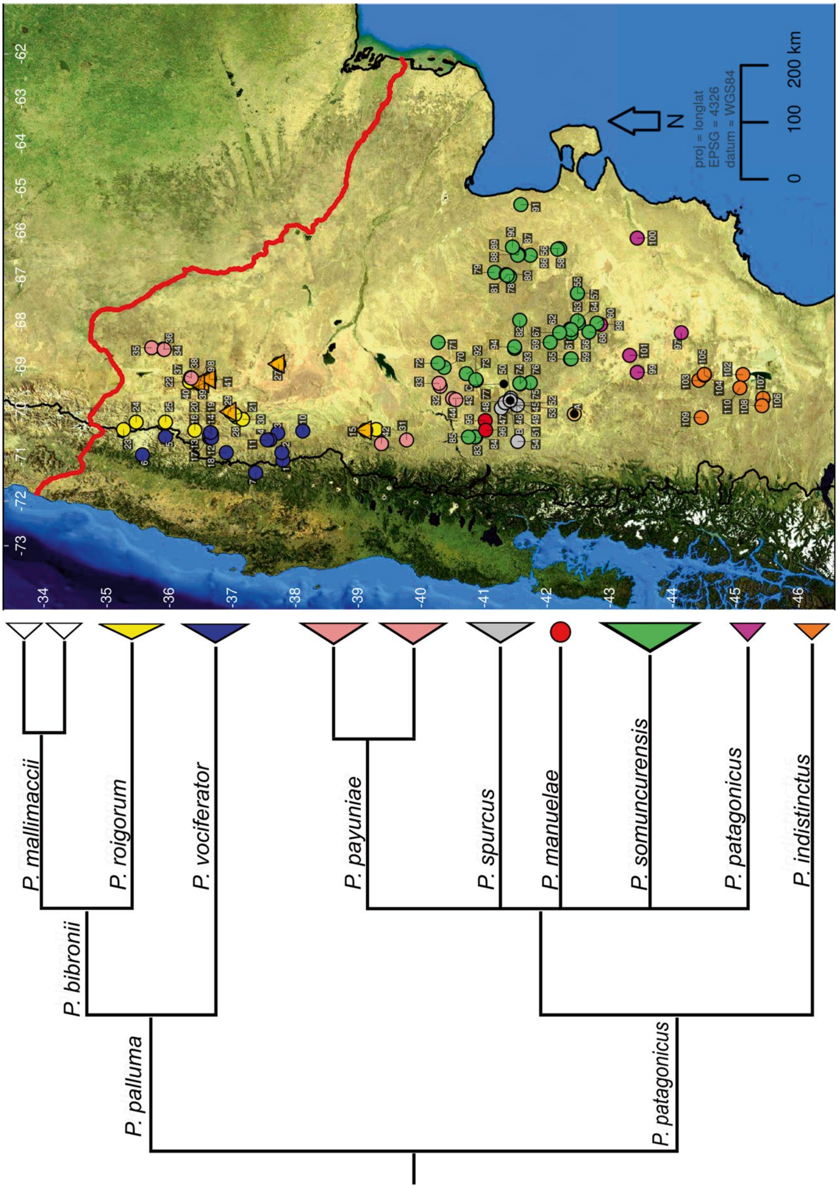
Clade	Localities	Individuals
L. chiliensis clade (subgenus)		
L. elongatus	129	525
L. petrophilus	129	498
L. kriegi	51	215
L. punmahuida	5	31
L. bibronii/gracilis	147	412
Eulaemus clade (subgenus)		
L. lineomaculatus	265	1710
L. darwinii	104	300
L. fitzingerii	382	2015
L. boulengeri	156	594
L. rothi	165	515
L. donosobarrosi	76	256

and reanalyses of the earlier molecular dataset inferred more candidate species (Lobo et al. 2016, 2018) and allowed some formal species descriptions (Chap. 7); the number of formally recognized *Phymaturus* species is presently 48, and this will certainly increase with additional study.

Several new *Phymaturus* candidate species hypotheses and their relationships are now available, based on updated phylogenies; the more recent ones include Lobo et al. (2016, 2018), Corbalán et al. (2016), Becker et al. (2019), and Esquerré et al. (2019a). We reviewed these studies, integrated all the georeferenced localities with voucher numbers, and summarized highly congruent taxonomic arrangements across these studies in Fig. 9.1. The *P. patagonicus* clade currently includes 25 described and 5 candidate species, whereas within the geographically more restricted *P. palluma* clade in Patagonia Argentina (northwestern Patagonia), the nested *P. roigorum* and *P. vociferator* clades include 7 described and 9 candidate species (although the topological position of *P. querque* is uncertain and currently cannot be included either in the *P. roigorum* or *P. vociferator* clades).

The lack of strong support for phylogenetic relationships among main species groups of the *P. patagonicus* clade (Fig. 9.1) may reflect still fragmentary knowledge, but also several aspects of these lizards' natural history may be involved, i.e., almost every population seems to be isolated on a volcanic outcrop, all have long generation times and females bear only 1 or 2 offspring every 2 years (Chap. 12), all are strictly herbivorous, and morphological stasis is the norm (Marín et al. 2018). Further, their divergence history possibly included several populations isolated in a short period of time around the Somún Curá plateau, which when coupled with their ecologically restricted habitat, may underlie a striking pattern inferred for their evolutionary diversification dynamics: high speciation rates coupled with high extinction rates (Olave et al. 2020b).

It is worth highlighting here some features of the *Phymaturus spurcus* clade. Individuals from very close localities (maximum range area is 40 km, Fig. 9.1, grey circles, locs. 45–53) have been recognized as four species (*P. spurcus*, *P. excelsus*, *P. spectabilis*, *P. agilis*), mainly based on morphological and coloration characters (Lobo and Quinteros 2005a, b; Scolaro et al. 2008). While another candidate species (*P.* sp. 13, Fig. 9.1, grey circle, loc. 54) from a nearby locality has been recognized on the basis of mtDNA (Morando et al. 2013), cyt-b sequences were almost identical among the first four species. Lobo et al. (2012) analyzed 10 individuals from the type locality of *P. agilis*, five of which had a bold pattern and other five a uniform pattern (the latter was considered representative of *P. spectabilis*). Further, one bold pattern female gave birth to two offspring, each with one of the alternative patterns. Lobo et al. (2012) also reanalyzed morphometric and meristic data used in the *P. agilis* species description (Scolaro et al. 2008), compared with the other related species and proposed that *P. agilis* is a junior synonym of *P. spectabilis*. Corbalán et al. (2016) mentioned that during three summers several females of various species of this group gave birth to different morphs (female of *P. spurcus* had offspring of *P. excelsus*, female of *P. excelsus* had offspring of *P. excelsus* and *P. spectabilis*). These authors, in agreement with Morando et al. (2013), revealed


P. mallimaccii
P. bibronii
P. roigorum
P. vociferator
P. palluma
P. payuniae
P. spurcus
P. manuelae
P. somuncurensis
P. patagonicus
P. indistinctus
P. patagonicus
-73
-72
-71
-70
-69
-68
-67
-66
-65
-64
-63
-62
-34
-35
-36
-37
-38
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-40
-41
-42
-43
-44
-45
-46
proj = longlat
EPSG = 4326
datum = WGS84
N
0 100 200 km

Fig. 9.1 Geographic distribution of *Phymaturus* species in Patagonia based on georeferenced localities with voucher numbers, arranged based on updated systematic studies summarized in tree on the left. Clades are color-coded with localities. The five localities where one species of the *palluma* and one of the *patagonicus* main clades are in sympatry are marked with orange triangles (8, 9, 15, 27, 28). Letters denote species never used in a phylogeny and/or dubious validity. A: *P. curivilcun*, B: *P. agilis* (synonymized with *P. spectabilis*), C: *P. desuetus* (described based on 1 individual). Locality numbers: ***P. palluma* main clade**: The *mallimaccii* subclade is distributed in Northwestern Argentina, beyond the scope of this review; *roigorum* clade (yellow circles), *P. roigorum* (22, triangles 8, 9), P. *verdugo* (23–25), *P. querque* (26, triangle 15), *P.* sp. 7 (triangle 27), *P.* sp. 8 (20), *P.* sp. 9 (21, triangle 29), *P. tromen* (28, 30); *vociferator* clade (violet circle), *P. dorsimaculatus* (1–4), *P. maulense* (5, 6), *P. vociferator* (7), *P.* sp. 3 (10), *P.* sp. 4 (11), *P.* sp. 5 (12), *P.* sp. 6 (13, 14, 16–19). ***P. patagonicus* main clade**: *indistinctus* clade (orange circles), *P. castillensis* (102), *P. felixi* (103–105), *P. indistinctus* (106–109), *P. videlai* (110); *patagonicus* clade (purple circles), *P.* sp. 14 (97), *P.* sp. 15 (98), *P. patagonicus* (99,100), *P.* sp. 1 (Corbalán et al. 2016) (101); *somuncurensis* clade (green circles), *P. calcogaster* (55–58), *P. camilae* (59–69), *P. ceii* (70–73), *P. etheridgei* (74–76), *P. sinervoi* (77), *P. somuncurensis* (78–82), *P. tenebrosus* (83–85), *P. yachanana* (86–91), *P.* sp. 20 (92), *P.* sp. 21 (93, 94); *P. manuelae* (95, 96); *spurcus* clade (grey circles), *P. spurcus* (45–53), *P. spectabilis* and *P. excelsus* distributed in this same have been proposed as synonyms of *P. spurcus* (Becker et al. 2019), *P.* sp. 13 (54); *payuniae* clade (peach circles), *P.* sp. 12 (triangle 8), *P. zapalensis* (triangle 15), *P. sitesi* (triangle 27), *P. delheyi* (triangle 29), *P.* sp. 17 (31), *P.* sp. 19 (32, 33), *P. nevadoi* (34–36), *P. payuniae* (37–41, triangle 9), *P. rahuensis* (42), *P. cacivioi* (43, 44) almost no variation among the first four species based on COI mtDNA data (Corbalán et al. 2016), and supported the observation of a very polymorphic population in this area with respect to coloration patterns (Avila et al. 2011, 2014). A recent study showed lack of statistical support with classical and geometric morphometric data for recognizing most of these species (as well as other closely related *Phymaturus* species, Marín et al. 2018). A detailed study on *P. verdugo* (a species in the *P. roigorum* group) showed extensive color polymorphism within a single population, suggesting that these characters may be highly variable on other *Phymaturus* species (Corbalán et al. 2018). Thus, a parsimonious interpretation is that these four names likely apply to one species (*P. spurcus*) with extensive color polymorphism. Indeed, almost simultaneously, Becker et al. (2019), based on mtDNA and coloration pattern analyses concluded that *P. spurcus*, *P. excelsus*, *P. spectabilis*, and *P. agilis* seem to be one highly structured species. Alternatively, but not completely mutually exclusive, Morando et al. (2013) observed some molecular incongruences among these species that suggested the possibility of hybridization among recently, partially isolated populations (Sect. 9.6).

Further, genetic distances between combinations of species' pairs within each of these *P. patagonicus* groups tend to be relatively low compared to studies on the *Phymaturus palluma* (northern) clade, based on the same gene regions (Morando et al. 2013; Lobo et al. 2018; Corbalán et al. 2016). Within the *P. patagonicus* group, morphological differences have been detected (Marín et al. 2018; Lobo et al. 2018), but clear diagnostic morphological characters are very scarce, and a stabilizing selection model has been proposed for the clade (Marín et al. 2018; Reaney et al. 2018). Lastly, in the context of this microendemic distribution pattern, unsampled geographic gaps still remain (Fig. 9.1), highlighting the need for further integrative morphological and genomic studies on species boundaries at small local scales where populations are often parapatrically distributed, to thoroughly test species hypotheses and geographic distributions.

Phylogeographic studies on the Patagonian Leiosaurae (Femenías et al. 2020) and Gekkota (Phyllodatylidae) species (unpublished data) generated new hypothesis for their species boundaries and demographic histories, some of them geographically concordant with various *Liolaemus* complexes (Sect. 9.4). However, regional comparative evolutionary patterns are just beginning, and future studies will be able to quantitatively assess levels of congruence.

In summary, these phylogeographic and phylogenetic studies reveal that our knowledge on lizard diversity in Patagonian Steppe at taxonomic, distributional, and phylogenetic levels (i.e., Linnean, Wallacean, and Darwinian shortfalls; Brito 2010; Diniz-Filho et al. 2013) is still largely incomplete; but now we have a glimpse of its magnitude and of the varied unexpected demographic and evolutionary processes that may have played a role in their diversification histories.

9.3 From the First Phylogeographic Studies to Denser Phylogenetic Trees

Since the Morando et al. (2003) first phylogeography paper on three related complexes representative of the main (subgenus) *Liolaemus* sensu stricto clade, subsequent studies focused on detailed analyses of each of these three Patagonian complexes. The *L. kriegi* complex was addressed based on further geographic sampling, coupled with morphological analyses (Medina et al. 2013) and the addition of a few nuclear regions as well as mtDNA (Medina et al. 2014, 2015). New species were described next to the western political border of the Andes with presence in Argentina (Fig. 9.2, yellow square 3, green square 4), and this complex presently includes five species and three candidate species (Fig. 9.2).

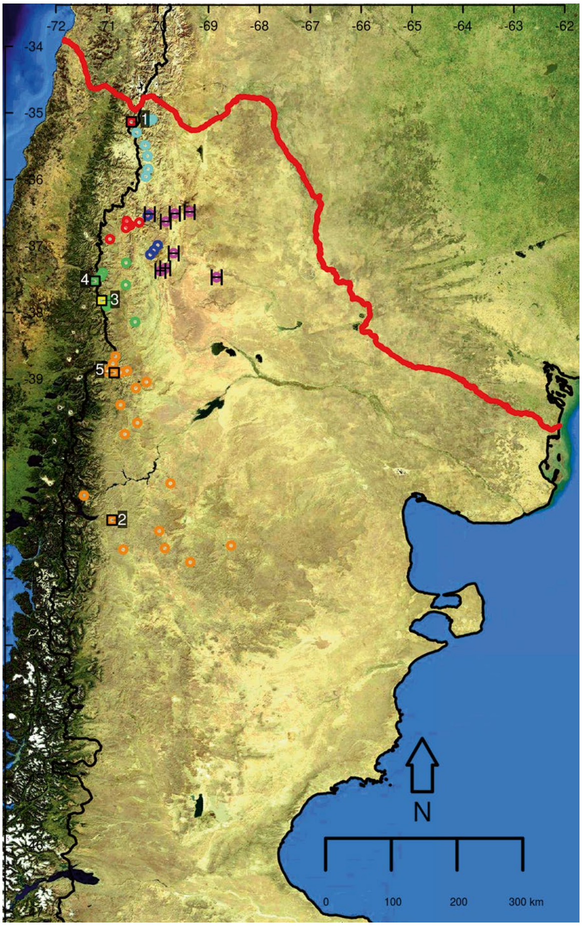

Fig. 9.2 Distribution area for the *Liolaemus kriegi* species group based on vouchered individuals used in phylogenetic and phylogeographic analyses. Numbers represent type localities and colored circles mark georeferenced localities for each recognized taxon; 1: *L. buergeri*, red; 2: *L. kriegi*, orange; 5: *L. ceii*, orange; 3: *L. tregenzai*, yellow; 4: *L. zabalai*, green; *L.* sp. B, magenta; *L.* sp. C, blue; *L.* sp. D, turquoise. The eight "H" correspond to the known distribution of *L.* sp. B for which all individuals have mt markers closely related to the *L. kriegi* species group and nuclear markers closely related to *L. autromendocinus* (see Fig. 9.3, light orange)

A more densely sampled phylogeographic study of the *L. elongatus* complex (Medina et al. 2017), coupled with new species descriptions (Abdala et al. 2010; Avila et al. 2010, 2012, 2015), increased the number of recognized species in Argentinean Patagonia to nine, plus three candidate species (Fig. 9.3). The *L. petrophilus* complex has seven species distributed north of Patagonia, and three in the Patagonian Steppe. Morando et al. (2003) found mtDNA evidence for two species within the species *L. petrophilus*, and Fontanella et al. (2012) confirmed this hypothesis based on phylogeographic patterns and climatic niche modeling (Fig. 9.4, green and blue circles). A later study (Feltrin 2013) found support for the recognition of two species within *L. austromendocinus* (Fig. 9.4, red and dark orange circles), separated by the Neuquén River, and detected paraphyly within *L. gununakuna* (Fig. 9.4, yellow circles).

These three related complexes (*L. kriegi*, *L. elongatus*, and *L. petrophilus*), constitute the *L. elongatus*-*kriegi* clade (also referred to as "group"), with other species distributed further west on the Chilean side of the Andes, and extending into northwestern Argentina (Medina et al. 2018). Alternative methods to infer phylogenetic history for the *L. elongatus*-*kriegi* clade (Medina et al. 2018), and results for this group within the more inclusive phylogeny of Pincheira-Donoso et al. (2019), do not share many strongly supported congruent results, but in general the *L. elongatus* and *L. kriegi* complexes appear to be sister groups, and the species *L. petrophilus* has an uncertain topological position within the group. A closely related group, the *L. punmahuida* clade that includes *L. punmahuida* (Fig. 9.4, loc. 5, turquoise square) and *L. flavipiceus* (Fig. 9.4, loc. 4, magenta square) seem to be the sister of the *L. elongatus* group (*L.* sp. 3 in Morando et al. 2003; Medina et al. 2018; Esquerré et al. 2019b). In general, the southernmost species of these three complexes (*L. kriegi*, Fig. 9.2, orange circles; *L. elongatus*, Fig. 9.3, blue circles; *L. petrophilus*, Fig. 9.4, blue circles) experienced recent range expansions, while the fragmented distributions of northwestern Patagonian species are likely due to river barriers (Colorado, Neuquén, Limay), and higher mountain peaks separated by valleys. Further, Pleistocene climatic cycles most probably contributed to episodic population isolations followed by local expansions; any combination of the above geographic/climatic scenarios could have promoted occasional interspecific gene flow (Sect. 9.6), thus contributing to "fuzzy" species boundaries detailed in Medina et al. (2014, 2017). Detailed genomic studies coupled with analyses of morphological variation will be needed for further progress to resolve the evolutionary histories of these groups.

9.4 From the First Qualitative Comparative Patterns to Filling in Geographic Gaps…and More Hidden Diversity

The first mtDNA-based phylogeographic studies of 15 Patagonian lizard species (Morando et al. 2003, 2004, 2007; Avila et al. 2006; Victoriano et al. 2008), in combination with data from similar studies on plants and rodents, were summarized in

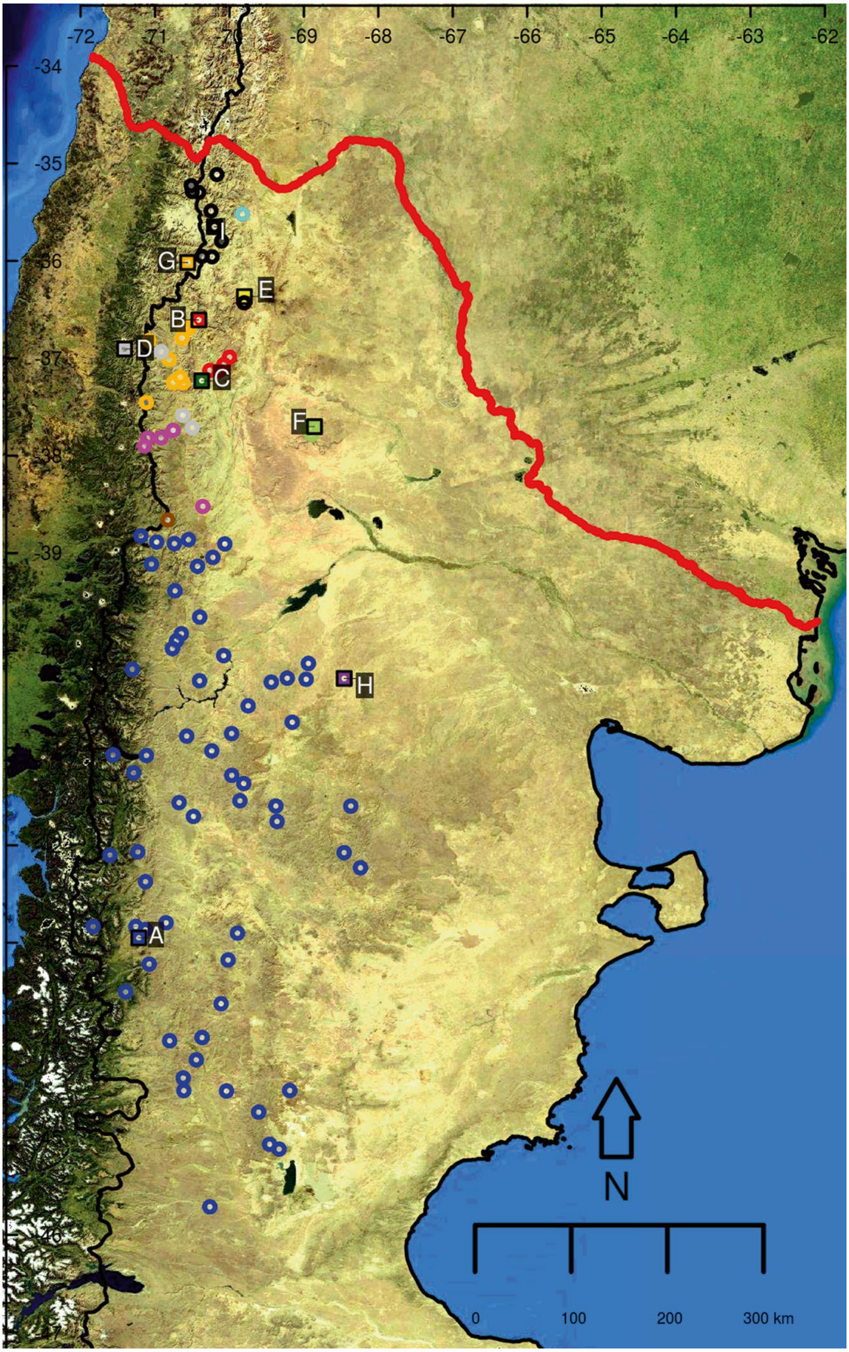

Fig. 9.3 Distribution area for the *Liolaemus elongatus* species group based on vouchered individuals used in phylogenetic and phylogeographic analyses. Letters represent type localities and colored circles mark georeferenced localities for each recognized taxon; A: *L. elongatus*, blue; B: *L. antumalguen*, red; C: *L. burmeinsteri*, darkgreen; D: *L. chillanensis*, grey; E: *L. choique*, yellow; F: *L. crandalli*, green; G: *L. carlosgarini*, darkgolden; H: *L. shitan*, purple; I: *L. smaug*, black; *L.* sp. 2, turquoise; *L.* sp. 3, brown; *L.* sp. 6, magenta

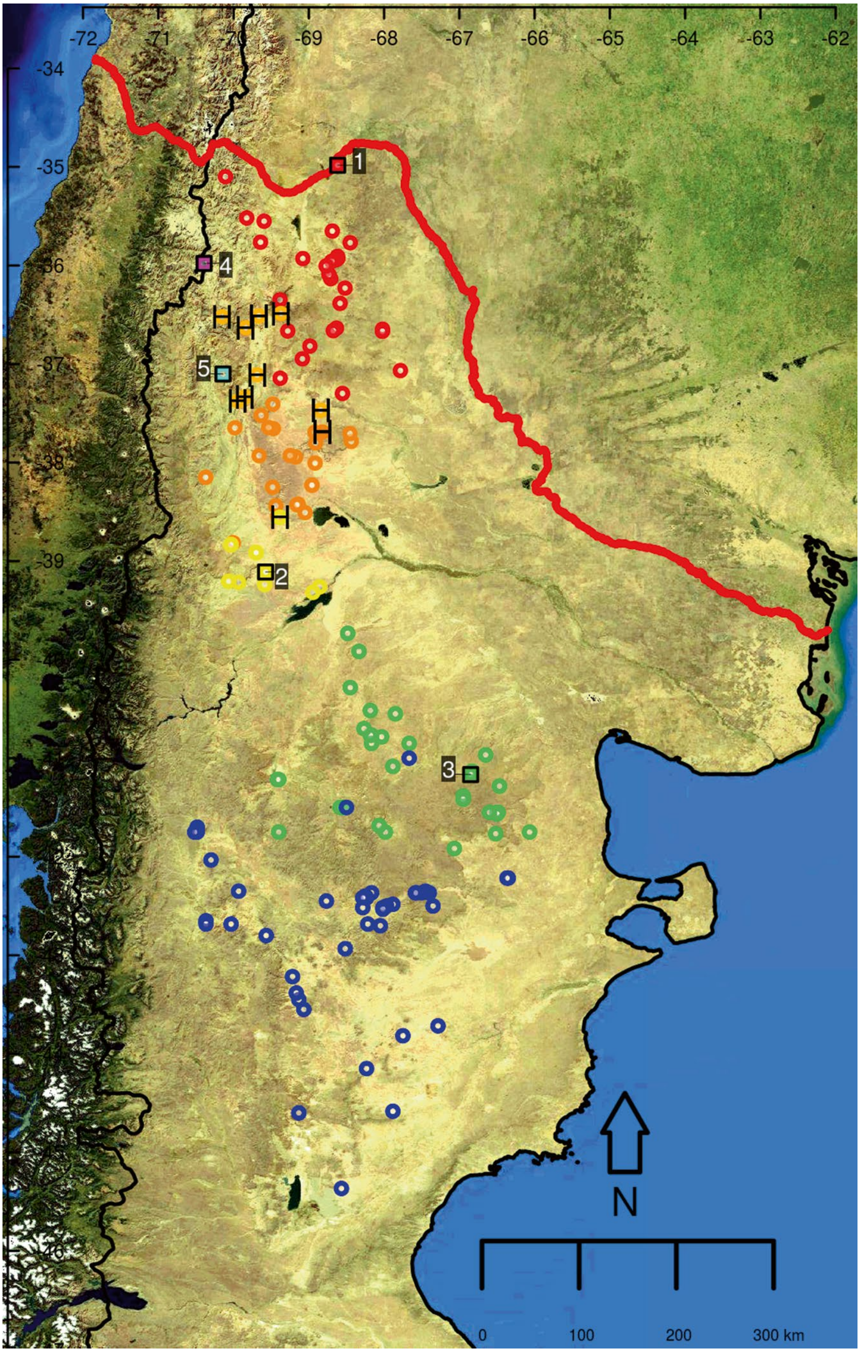

Fig. 9.4 Distribution area for the *Liolaemus petrophilus* species group based on vouchered individuals used in phylogenetic and phylogeographic analyses, and for the *L. punmahuida* clade. Numbers represent type localities and colored circles mark georeferenced localities for each

Sérsic et al. (2011). This review highlighted several issues for lizards: 1—data were very limited for Patagonia's "Deep South" (mainly southern Chubut and Santa Cruz provinces); 2—the area between northern Neuquén and southern Mendoza province (35 to 37° S), and the coastline of Río Negro and Chubut Provinces were identified as high biodiversity regions; 3—a possible valley refugium was identified in the Andean region in northwestern Patagonia, 4—several phylogenetic breaks were identified, most approximately concordant with main river basins and one with the Somún Curá Plateau (Fig. 2 in Sérsic et al. 2011); 5—in northwestern Patagonia where the Andes increase in altitude, landscapes compose a highly fragmented area, and some prominently east-to-west postglacial migration routes were identified, and north-to-south migrations were inferred in parallel with coastline shifts in northern Patagonia (Fig. 4 in Sérsic et al. 2011); and 6—the ecotone between Monte and Patagonian Steppe regions, the coastline of southern Río Negro and Chubut, and southeastern Chubut were identified as regions of secondary contact between some lizard species.

The knowledge gap for extreme southern Patagonia was first addressed by Breitman et al. (2012) in a study focused on one of the main groups within the *L. lineomaculatus* section: the *L. lineomaculatus* group (Fig. 9.5, green dots). This group originally included four described species, but Breitman et al. uncovered several geographically structured genetic lineages, some of which were hypothesized as candidate species, and two of these were later formally described (Breitman et al. 2011a, b). Breitman et al. (2012) resolved a predominantly latitudinal pattern of population structure, with some phylogeographic breaks concordant with those previously proposed for plants and rodents (Fig. 4 in Breitman et al. 2012). Previous lizard phylogeographic data for this region were very limited (4 species: the southernmost part of *L. elongatus* [Fig. 9.3, blue dots] and *L. kriegi* [Fig. 9.2, orange dots] in western Chubut, and the southeastern part of *L. bibronii* [Fig. 9.6] and *L. fitzingerii* [Fig. 9.10]), and showed a clear pattern of recent range expansion and low nucleotide diversity. In contrast, the pattern resolved by Breitman et al. (2012) in the *L. lineomaculatus* group was strikingly different, revealing unexpectedly high genetic diversity (haplotype and nucleotide indices), and almost no evidence of demographic changes. This pattern suggested that some of these lineages might have survived in previously hypothesized (for plants) peripheral refugia near glacial areas (Sérsic et al. 2011) at latitudes 46°–52° S.

This southernmost part of Patagonia is also inhabited by lizards of the *L. kingii* clade (Fig. 9.5, orange dots), and phylogeographic analyses (Breitman 2013)

◄

Fig. 9.4 (continued) recognized taxon; 1: *L. austromendocinus*_Mza, red; *L. austromendocinus*_Nq, dark orange; 2: *L. gununakuna*, yellow; 3: *L. petrophilus*_N, green; *L. petrophilus*_S, blue; *L.* sp. B, light orange. *Liolaemus punmahuida* clade, 4: *L. flavipiceus*, magenta; 5: *L. punmahuida*, turquoise. The eight "H" on top of light orange circles correspond to the known distribution of *L.* sp. B for which all individuals have mt markers closely related to the *L. kriegi* species group and nuclear markers closely related to *L. autromendocinus* (see Fig. 9.2, magenta). The "H" on top of the yellow circle represents individuals for which gene flow was detected between *L. gununakuna* and *L. austromendocinus*_Nq

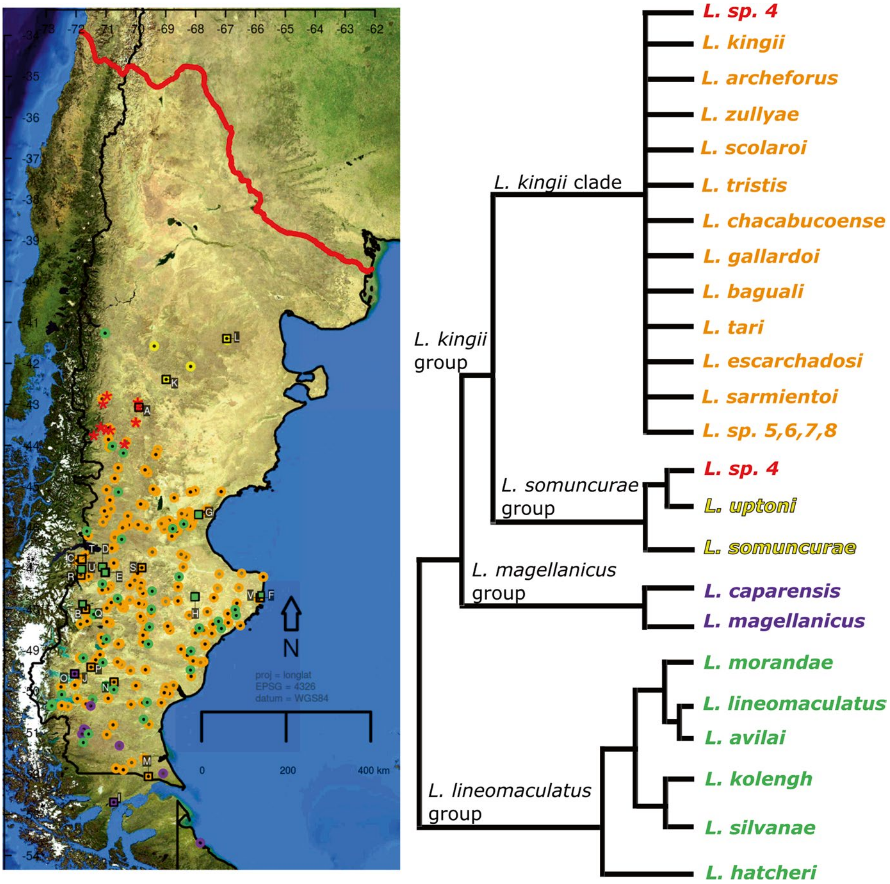

Fig. 9.5 Distribution area for the *Liolaemus lineomaculatus* section based on vouchered individuals used in phylogenetic and phylogeographic analyses. Letters represent type localities and colored circles mark georeferenced localities. The *L. lineomaculatus* species group is colored in green: B, *L. hatcheri*; C, *L. kolengh*; D, *L. silvanae*; E, *L. avilae*; F, *L. lineomaculatus*; G, *L. morandae*; H, *L. yatel*. The *L. magellanicus* species group is colored in purple: I, *L. magellanicus*; J, *L. caparensis*. The *L. somuncurae* species group is colored in yellow: K, *L. uptoni*, L, *L. somuncurensis*. The *L. kingii* species group is colored in orange: M, *L. sarmientoi*; N, *L. escarchadosi*; O, *L. tari*; P, L. *baguali*; Q, *L. gallardoi*; R, *L. chacabucoense*; S, *L. tristis*; T, *L. zullyae*; U, *L. archeforus*; V, *L. kingii*. Letter A, red stars: L. sp. 4, for which all individuals have mt markers closely related to the *L. somuncurae* species group and nuclear markers closely related to the *L. kingii* species group (Breitman et al. 2011a, b, 2015). *Liolaemus yatel* has not yet been included in any phylogenetic analyses

Fig. 9.6 (continued) square and red circles show distribution) and *L. gracilis*, magenta circles (A type locality in error); B: type locality of *L. cyaneinotatus*, dark orange square, only known from its type locality. Based on Martínez (2012) Bayesian delimitation method, hypothesis of different species within the *L. bibronii* complex: *L.* sp. 1, yellow; *L.* sp. 3, light green; *L.* sp. 4, blue; *L.* sp. 5, cyan; *L.* sp. 6, light orange; *L.* sp. 7, dark green; (*L.* sp. 2 was described as *L. cyaneinotatus*). The six "H" indicate areas where hybrids between *L. bibronii* and *L. gracilis* have been detected (Morando et al. 2007; Olave et al. 2011)

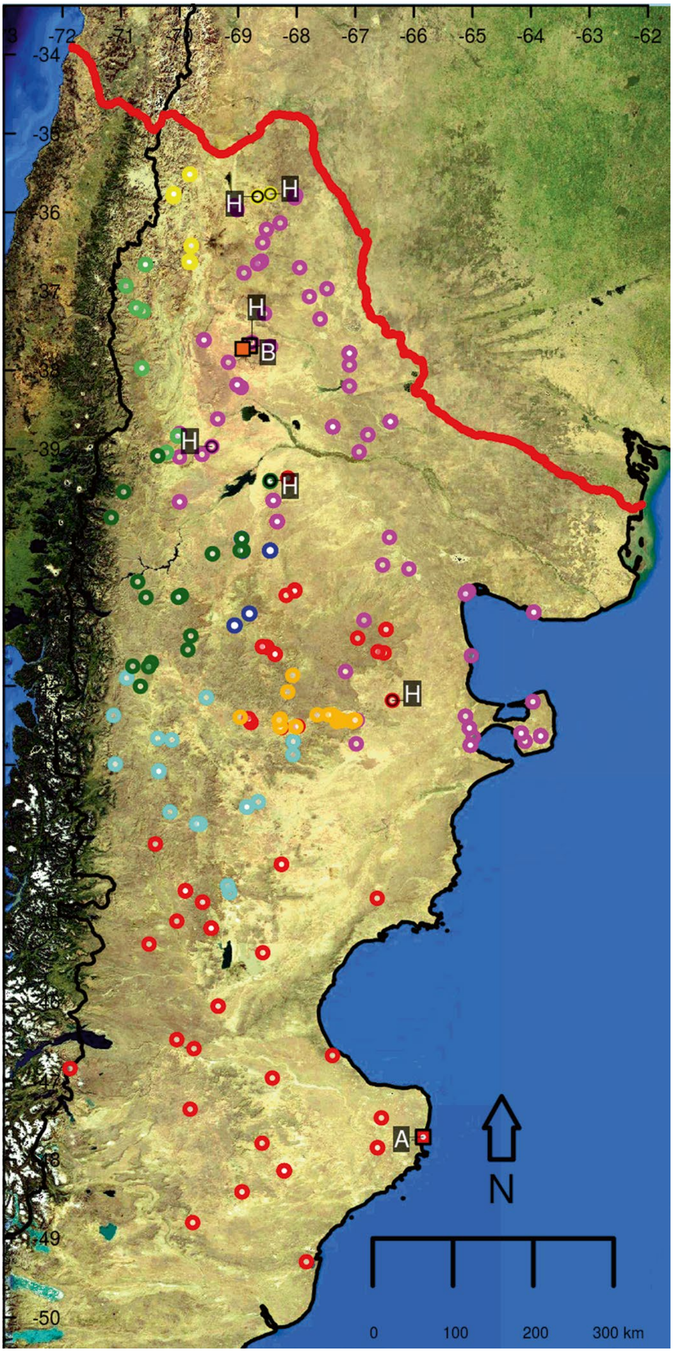

Fig. 9.6 Distribution area for the *L. bibronii* species complex and *L. gracilis*, based on phylogenetic and phylogeographic analyses. A: type locality of *Liolaemus bibronii* (sensu stricto, red

inferred five candidate species, and resolved unusually high mtDNA diversity with no clear geographic structure, but without strong support for phylogenetic relationships among its 11 closely related described species (Breitman et al. 2011a, b). The four southernmost distributed species of this group (*L. baguali*, *L. escarchadosi*, *L. sarmientoi*, and *L. tari*, Fig. 9.5, type localities P, N, M, and O, respectively) were the focus of an integrative study by Breitman et al. (2015). They used morphological data, mtDNA, and climatic niche envelopes to characterize these taxa (plus one related candidate species) and test species boundaries. Although some morphometric and meristic characters were found to differ among species, no qualitative morphological differentiation was detected, highlighting the challenging scenario for species delimitation in this group. Although some studies found statistical support for some relationships among a subset of these species (Espinoza et al. 2004; Pincheira-Donoso et al. 2019), these results are not congruent. We consider that both species boundaries and relationships remain unresolved for this clade; an integrative study including genomic data is now in progress (Sánchez, unpublished) should resolve many of these issues.

Another related group is the *L. somuncurae* clade that includes two described and one candidate species, *L.* sp. 4. This entity is particularly interesting as the mitochondrial locus places it within this group, while the nuclear loci place it within the *L. kingii* clade (Breitman et al. 2011a, b; Fig. 9.5, red stars; see further details in Sect. 9.6). A detailed phylogeographic and morphological study of the *L. somuncurae* clade (Breitman et al. 2015) clearly supported these three species and identified further genetic structure within *L.* sp. 4 that may represent independent lineages.

9.5 From the First Phylogeographic Steps to Multilocus Species Delimitation Methods: Coalescent and beyond

A mtDNA phylogeographic study of *L. bibronii*, a species widely distributed over almost all Patagonia (Morando et al. 2007, $n = 138$ samples from 41 localities), resolved 12 independent lineages, with almost completely allopatric distributions. Several of these lineages were geographically concordant with haploclades detected in earlier phylogeographic studies of other species (Morando et al. 2003; Avila et al. 2006). To test the hypotheses that these lineages may represent different species, we initiated a follow-up study with denser sampling ($n = 415$ samples from 156 localities), multilocus data (2 mt, 4 nuc), and implementing several species delimitation methods (Martínez 2012). Here, the mtDNA gene tree inferred seven more lineages from previously unsampled areas; one of these is from the isolated Auca Mahuida region, and is now formally described as *L. cyaneinotatus* (Martínez et al. 2011). The tree-based Wiens and Penkrot (2002) method resolved 22 lineages as candidate species (although 8 were weakly supported), while a multispecies coalescent method (BPP; Yang and Rannala 2010) resolved six species besides the nominal *L. bibronii* and *L. cyaneinotatus* (not all lineages could be tested with this method, as some had low sample sizes, Fig. 9.6). Although multivariate morphometric and geometric morphometric analyses were not conclusive, they showed that the southernmost distributed nominal *L. bibronii* clade occupies a broad morphospace, suggesting high phenotypic plasticity, while populations in northwestern Patagonia tend to occupy smaller sections of the morphospace. Recently developed species delimitation methods that integrate molecular and morphological data (e.g., Solís-Lemus et al. 2017) are needed in order to explicitly test these species hypotheses.

The species *Liolaemus darwinii* occupies extensive geographic areas in sandy habitats in the southern and central portions of the Monte Desert in Argentina (Etheridge 1993). The first phylogeographic study (mtDNA) of this complex (Morando et al. 2004) resolved geographically structured genetic variation, evidence of demographic range expansions in its southernmost distribution area corresponding to northern Patagonia (Fig. 9.7, green circles), and some evidence of interspecific gene flow with *L. grosseorum* (Fig. 9.7, purple circles). It was therefore referred to as the *Liolaemus darwinii* complex. Technological advances made the sequencing of nuclear markers cost-effective, while the development of new analytical tools leads to statistical phylogeographic studies (Knowles 2009). The *L. darwinii* complex served as a model system for comparative tests of accuracy and precision of three coalescent-based methods (BPP, SpeDeSTEM, ABC), relative to the delimitation of species boundaries in this complex (Camargo et al. 2012b). Some of these methods can accommodate paraphyletic species and gene tree discordance, but not post-divergence gene flow, while others can incorporate gene flow. Based on two mtDNA and three nuclear markers, Camargo et al. (2012b) showed that all methods supported the distinctness of *L. darwinii* and *L. grosseorum* despite gene exchange, and that overall BPP was the most accurate, while ABC was the most flexible. See also Camargo et al. (2012a) for accuracy and precision of species tree under different sampling conditions, based on 20 loci from the *L. darwinii* species group.

To test the range expansion hypothesis for *L. darwinii* in the Monte region of northern Patagonia, Camargo et al. (2013) used mtDNA and 14 nuclear loci to apply a new diffusion dynamics method, a spatio-temporal phylogeographic reconstruction, that infers the geographic location of ancestors, and allows decoupling demographic from geographic expansion, thus it can be directly compared with paleo-distribution models (e.g., ENM). Results suggested a restricted range of *L. darwinii* in northwestern Patagonia (Río Negro Province) in the mid-Last Interglacial (ca. 95 ka), an area predicted as suitable for the species at 120 ka. Subsequently, multiple long-distance colonizations increased the distribution of *L. darwinii* to the west and southeast between 95 and 55 ka, and population size began its major southeastern expansion in a high-suitability region until the Last Glacial Maximum (LGM). More recently, the distribution range between the LGM up to the present showed modest increases, coupled with a large increase in population size. This paleo dynamic model of expansion is temporally and geographically congruent with fossil evidence (Chap. 6), and highlights the influence of climatic cycles on the population historical dynamics. Similar demographic expansion

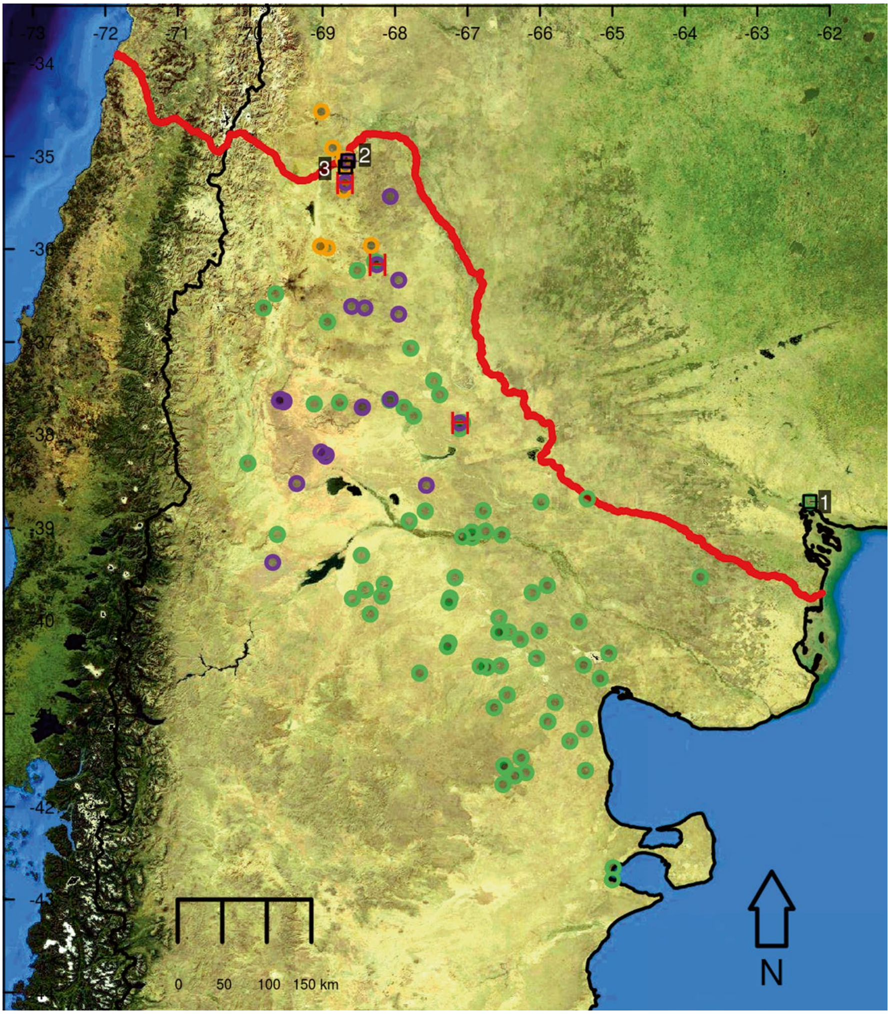

Fig. 9.7 Distribution area for *Liolaemus darwinii*, *L. grosseorum* and *L. parthenos*, based on phylogenetic and phylogeographic analyses. Numbers represent type localities and colored circles mark georeferenced localities for each taxon. 1, *L. darwinii*, green; 2, *L. grosseorum*, purple; 3, *L. parthenos*, orange. The 3 red "H" localities show sites where *L. darwinii* X *L. grosseorum* hybrids were found (Morando et al. 2004; Camargo et al. 2012a, b)

patterns before the LGM were inferred for the co-distributed species *L. gracilis* (Olave et al. 2011) and *Aurivela longicauda* (Yoke et al. 2006).

The first phylogeographic work for species of the *Eulaemus* clade (subgenus) (Avila et al. 2006) targeted several groups, and used two mtDNA and two nuclear gene fragments. This study resolved populations under the name *L. rothi* that could represent candidate species, but all were in need of detailed integrative studies. This study also showed that species boundaries were not clear, specifically with respect to some taxa of the *L. boulengeri* complex. A later morphological study (Abdala 2007) showed that some species of these two complexes were interdigitated. Abdala et al. (2012) further highlighted that they previously confused *L. purul* (described in that study) with *L. loboi*, and *L. tromen* with *L. hermannunezi*; we consider *L. purul* as part of the *L. rothi* complex (unpublished data). Olave et al. (2017) resolved 13 loci (mtDNA and 12 nuclear) and morphological data for analysis with the integrated multi-coalescent species delimitation program (iBPP, Solís Solís-Lemus et al. 2017) to statistically evaluate independent evolving lineages within the *L. rothi* complex. Eight lineages (1 undescribed, *L.* sp. 4) had strong statistical support and were inferred in two groups. One of these includes four species distributed in the higher Andes and pre-cordillera (a term used to define lower altitude mountain ranges close by and related to the Andes) (Fig. 9.8, *L. tromen*—yellow, *L.* sp. M34—green, *L. hermanunnezi*—blue, *L. loboi*—orange circles); three of these had slower rates of morphological evolution (smaller morphological support values) and evidence of stasis for smaller body sizes, compared to the second group. This second group included the other four species distributed in more Steppe habitats (Fig. 9.8, *L. sagei*—turquoise, *L. sitesi*—dark green, *L. rothi*—red, *L.* sp. 4—white circle) had strong statistical support; they are characterized by larger body sizes likely maintained by stabilizing selection.

The same phylogeographic study of Avila et al. (2006) also focused on several populations under the name *L. boulengeri* that resolved several paraphyletic lineages interdigitated with lineages of *L. rothi* (Sect. 9.6) and it was clear that knowledge of species boundaries was very limited. As mentioned in the previous paragraph, Abdala (2007) based on morphological characters inferred a more inclusive group (he named *L. melanops* group = to *L. melanops* series of Fontanella et al. 2012) that included all the species of the *rothi*, *boulengeri*, *cuyanus/donosobarrosi*, and *fitzingerii/melanops* complexes interdigitated. This is an expected result considering the high level of hybridization that seems to occur among species of these complexes (Sect. 9.6). Similarly, Olave et al. (2014) included a wide geographic sampling of populations that could be assigned to *L. rothi* and *L. boulengeri*, used 14 loci and different methods of phylogenetic inference and newer species tree approaches. The confusion about these complexes was evident as 20 independent lineages were inferred; 12 of these were called *L.* sp., and some appeared paraphyletic between these two species complexes. Figure 9.9 depicts the five species that we include in the *L. boulengeri* complex whose distributions do not seem to extend north of the Limay River. The distribution of *L. boulengeri* (orange circles) includes an undescribed species in the southeastern part of its range—northeastern Santa Cruz Province (Avila et al. 2008a). Given the resolved complexity of species of these complexes, especially in northern Patagonia where current data show several instances of hybridization (Sect. 9.6), an ambitious integrative large-scale study is needed in order to test and refine the real species diversity, identify evolutionary, and demographic processes underlying their phenotypic polymorphisms, and complete a map of hybrid zones.

The main taxonomic focus of Avila et al. (2006) was the *L. fitzingerii* group, which at the time included *L. canqueli*, *L. cuyanus*, *L. donosobarrosi*, *L. fitzingerii*,

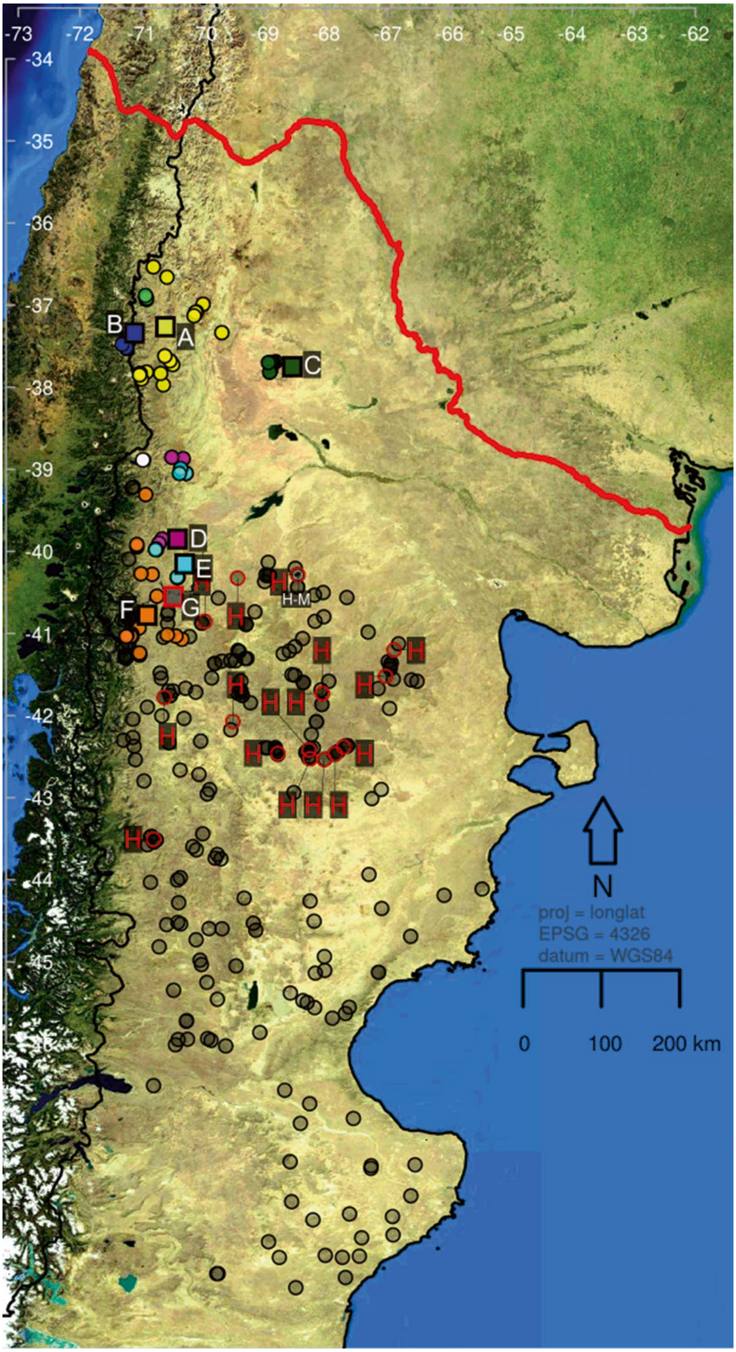

Fig. 9.8 Distribution area for the *Liolaemus rothi* species group based on phylogenetic and phylogeographic analyses. Letters represent type localities and colored circles georeferenced localities

L. martorii, *L. melanops*, *L. morenoi*, and *L. xanthoviridis*. Avila et al. inferred these species into three clades they identified as: (1) the *L. melanops* complex: including individuals from *L. canqueli, L. martorii*, *L. melanops*, and *L. morenoi* grouped into two main clades geographically concordant but not with previous knowledge of these species distributions; (2) the *L. fitzingerii* complex: *L. fitzingerii* and *L. xanthoviridis*; and (3) the *L. donosobarrosi* complex: *L. donosobarrosi*, *L. cuyanus* (including two independent lineages), and three candidate species. The *L. melanops* and the *L. fitzingerii* complexes inferred as sister clades, now referred as the *L. fitzingerii* group (Fig. 9.10), is congruent with the morphological study by Abdala (2007) based on total evidence tree that named all these species in a "*fitzingerii* clade". Phylogeographic inferences made by Avila et al. (2006) included: (1) range expansions for the southernmost distributed populations (Fig. 9.10, blue, green, and yellow dots); (2) genetically diverse and strongly structured populations distributed in a narrow north-south strip (43°–45°) between the coastline and the Montemayor plateau (Fig. 9.10, between Peninsula Valdés and Type locality K); and (3) two zones of secondary contact were hypothesized (Fig. 9.10, letter K and yellow dot with an H in the northern coastline). Olave et al. (2014) based on 14 loci did not find support for phylogenetic relationships between these species (including also *L. chehuachekenk* described in Avila et al. 2008b), except that all of them plus some unnamed taxa form a clade, the *L. fitzingerii* group. Thus, even with 14 loci, no strong relationships were inferred and also species boundaries remained "fuzzy". In the first genomics study of the genus, Grummer et al. (2018) resolved 580 nuclear loci for 27 individuals representative of this group, and resolved support only for a (*L. fitzingerii* + *L. xanthoviridis*) clade. However, Phylonet (Than et al. 2008) analyses identified several instances of interspecific gene flow among several of these species (Sect. 9.6). Further, Grummer (2017) based on ~900 SNPs from 178 samples found evidence for six genetically different populations within the *L. fitzingerii* group. These species are morphologically highly polymorphic (Minoli et al. 2014, 2016), as well as in the extent of their melanism (Escudero et al. 2012). Further, one population of *L. xanthoviridis* was later found to vary ontogenetically in the extent of its melanism (Escudero et al. 2016). We suggest that thus, now it is clear that these species do not have "hard" boundaries, cannot be called "boundaries" and their evolutionary history probably included many repeated instances of hybridization among previously isolated populations. This history may have been driven by climatic oscillations as these divergences were inferred to have occurred during the last 2 Ma (Olave et al. 2015; Grummer 2017).

The *Eulaemus* gene tree of Avila et al. (2006) was congruent with the mtDNA parsimony tree (Schulte et al. 2003) and a total evidence analysis (Abdala 2007) in that the first split after the divergence of the *L. lineomaculatus* section was the

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Fig. 9.8 (continued) for each taxon. A, *L. tromen*, yellow; B, *L. hermannunezi* (outside the political boundaries of Argentina), dark blue; C, *L. sitesi*, dark green; D, *L. purul*, dark pink; E, *L. sagei*, turquoise; F, *L. loboi*, orange; G, *L. rothi*, red; *L.* sp. M34, green; *L.* sp. 4, white. Grey circles correspond to the distribution area of *L. boulengeri* species group (Fig. 9.9) intending to show its overlap in the northern area with *L. rothi* (red circles) with which it hybridizes extensively, red "H" (Olave et al. 2018). The "H-M" symbol marks a locality where a mosaic individual (1/3 of analyzed cells were triploid and 2/3 were diploid) was found (Morando 2004)

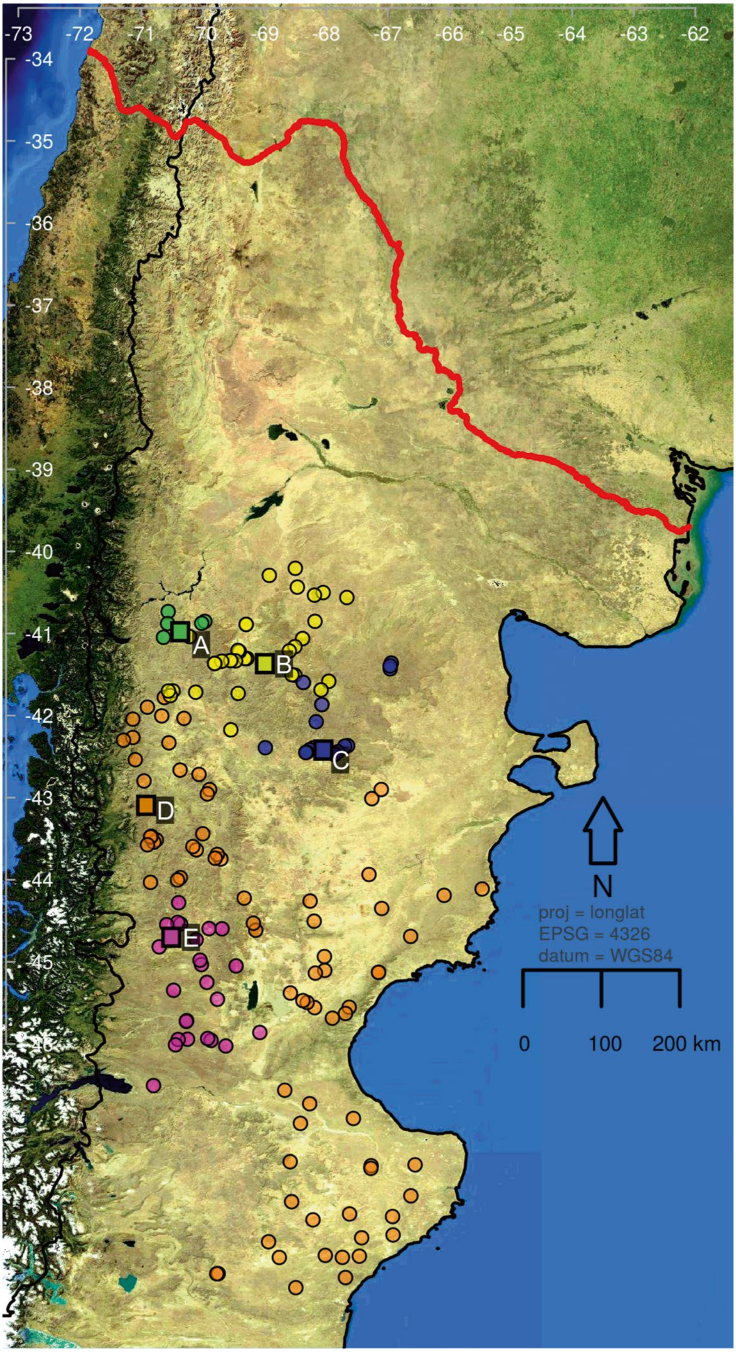

Fig. 9.9 Distribution area for the *Liolaemus boulengeri* species group based on phylogenetic and phylogeographic analyses. Letters represent type localities and colored circles mark georeferenced localities for each taxon. A, *L. tehuelche*, green; B, *L. inacayali*, yellow; C, *L. telsen*, dark purple; D, *L. boulengeri*, orange; E, *L. senguer*, dark pink

L. montanus group. However, these studies did not find strong support for relationships between the other main clades within *Eulaemus* (*L. wiegmannii*, *L. darwinii*, *L. anomalus*, *L. rothi*, *L. boulengeri*, *L. fitzingerii*, and *L. donosobarrosi* groups). Further, the gene tree of Avila et al. (2006) had very short internodes. Olave et al. (2014), based on 14 loci, also failed to find strong support for relationships among these groups, which led to developing a model-based approach to test the hypothesis of hard polytomies, assuming at least one or two extremely rapid radiations for these groups. Olave et al. statistically tested eight different topologies (based on all published alternative hypotheses for these groups), and although the "two polytomy" hypothesis had the highest support value, the "one polytomy" hypothesis was very close in value. If two divergence events occurred in a short period of time, then previously incongruent hypotheses are expected. Traditional phylogenetic methods assume hierarchical relationships only, so interspecific gene flow, especially if common, is expected to produce incongruent results. Given that hybridization seems to be prevalent in this genus (Sect. 9.6), most probably this process explains the lack of strongly supported resolution for relationships between these clades. A recent genomic approach (Morando et al. 2020) based on 584 loci, found strong support for most relationships among main clades within *Eulaemus*. The *boulengeri*, *rothi*, *fitzingerii* and *donosobarrosi* groups were inferred as a clade, but relationships among them were not strongly supported. This study also applied a new method that incorporates reticulation into coalescent models (Solís-Lemus et al. 2017) and detected two instances of past hybridation edges among main *Eulaemus* clades.

9.6 The "Promiscuous" Ones and the Successful Generalist Hypothesis

The first hint of introgression in Patagonian lizards was hypothesized by Morando et al. (2004), which detected three *L. grosseorum* individuals with cyt-b haplotypes diagnostic of the sympatric species *L. darwinii*-S, in northwestern Patagonia (Fig. 9.11). This same study found that the only Pleurodont parthenogenetic species, *L. parthenos* (at that time *L.* sp. nov., Fig. 9.7, orange circle with "H"; Fig. 9.11, pink with orange border stars), carried cyt-b haplotypes closely related to *L. darwinii*-S, but noted that its morphological features placed it in the *L. boulengeri* complex, whose current northernmost distribution is further south. The formal description of *L. parthenos* (Abdala et al. 2016) included a high-quality karyotype that showed it to be a triploid species ($3N = 49$), adding further evidence for its hybrid origin between *L. darwinii* and *L. boulengeri* lineages. Three additional *Liolaemus* species may also have hybrid origins: 1—Morando et al. (2003) identified *L.* sp. B (Fig. 9.11, yellow stars) within the *L. kriegi* group with mitochondrial data, but noted that its morphology corresponds to *L. austromendocinus*, and its geographic distribution is between these two species groups (Fig. 9.4, light orange circles with letter "H" and Fig. 9.2, pink circles with letter "H"). Subsequently,

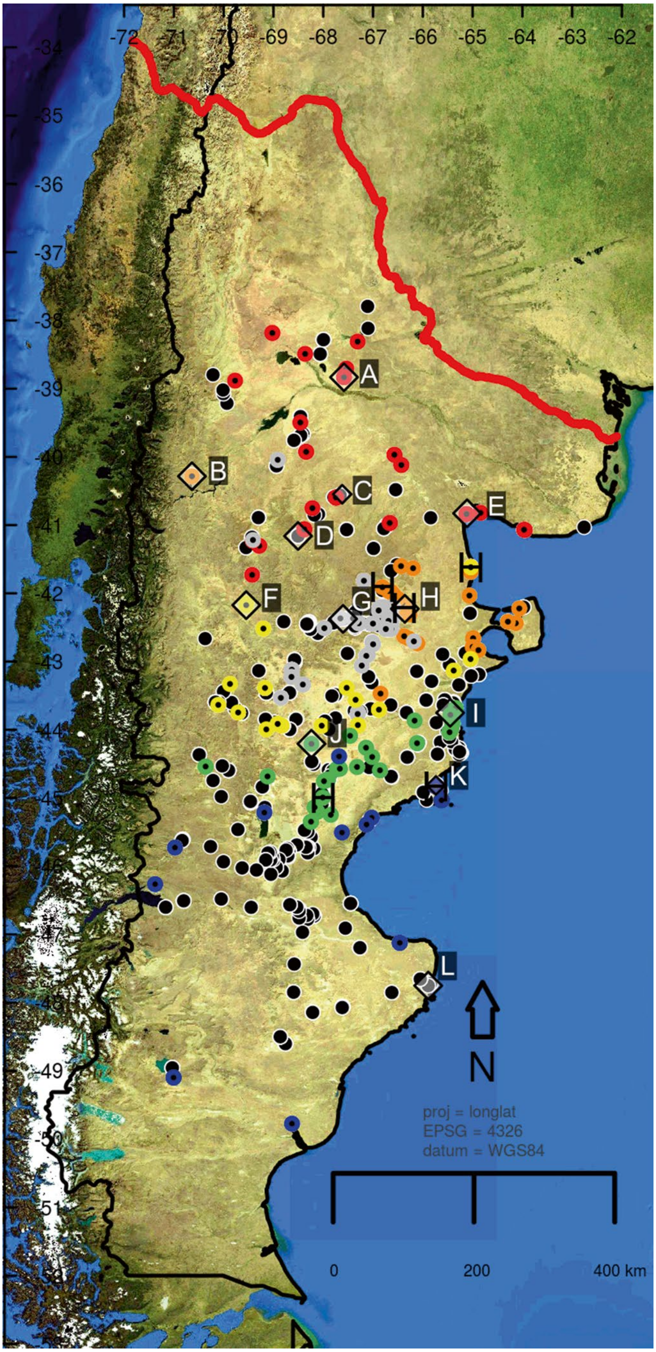

Fig. 9.10 Distribution area for the *Liolaemus fitzingerii* species group based on phylogenetic and phylogeographic analyses, represented with dark blue circles. Based on genomic ~900 SNPs, Grummer (2017) inferred 6 groups, color-coded and corresponding to different combinations of the 12 available species names: 1-blue, *L. camarones*, *L. fitzingerii*; 2-green, *L. xanthoviridis*; 3-yellow, *L. canqueli*, *L. chehuachekenk*, *L. melanops*, 4-grey, *L. shehuen*, *L. canqueli*; 5-orange, *L. martorii*, *L. melanops*; 6-red: L. *casamiquelai*, *L. dumerili*, *L. goetschi*, *L. martorii*, ambiguous:

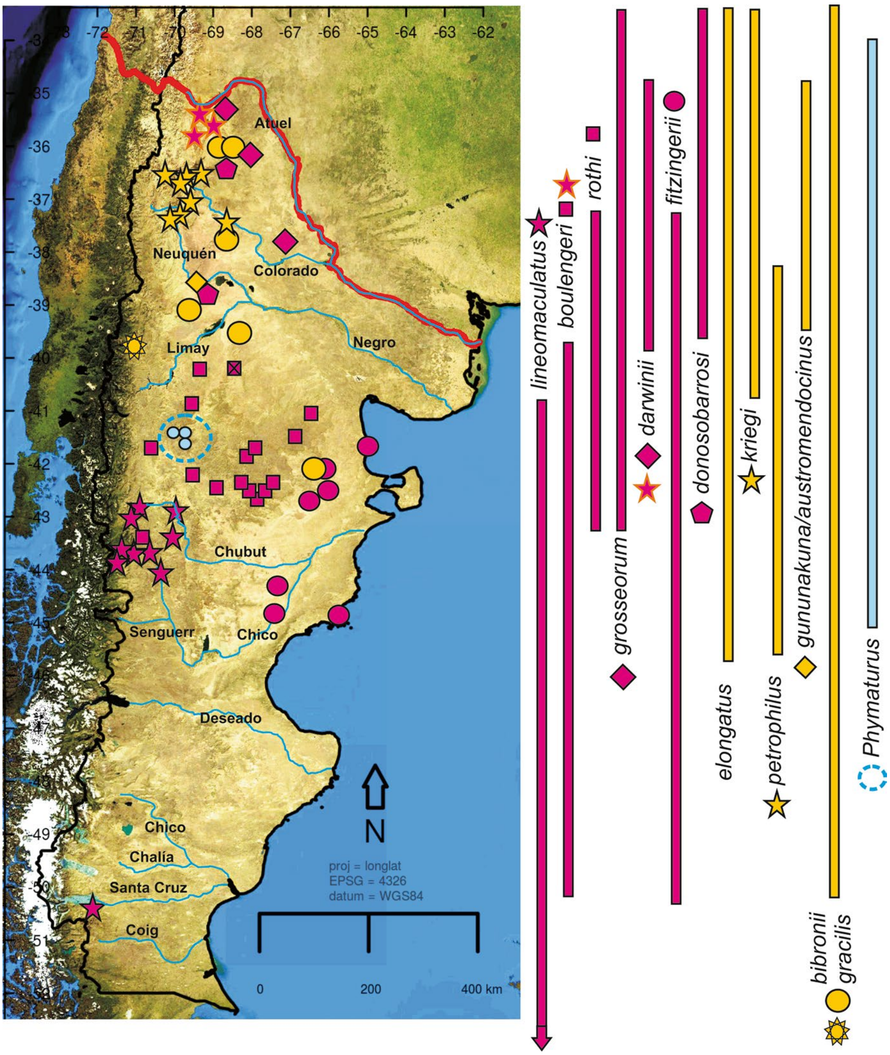

Fig. 9.11 Hybridization hypotheses in *Liolaemus*. Main *Eulaemus* clade: purple, *Liolaemus* sensu stricto: yellow. Stars: populations/species of possible hybrid origin. Yellow star with 12 points: *L. abdalai*. Purple stars with orange border: *L. parthenos*. Pink square with "X": *L. rothi* mosaic individual with diploid and triploid cells. Circles, squares, rhomboids, and pentagons: localities were interspecific gene flow has been detected. Light blue: sympatric and/or closely distributed *Phymaturus* species where gene flow has been hypothesized

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Fig. 9.10 (continued) B. L. morenoi. Rhomboid shapes with letters correspond to type localities of the 12 species described within this group. A. *L. goestchi*; B. *L. morenoi*; C. *L. dumerilii*; D. *L. casamiquelai*; E. *L. martori*; F. *L. chehuachekenk*; G. *L. shehuen*; H. *L. melanpos*; I. *L. xanthoviridis*; J. *L. canqueli*; K. *L. camarones*; L. *L. fitzingerii*. Rhomboids C and K have smaller sizes to identify recent morphological analyses that did not find support for the validity of these species (Minoli et al. 2014, 2016). The five "H" symbols indicate areas where hybrids have been detected (Avila et al. 2006; Morando et al. 2009; Grummer et al. 2018; Grummer 2017) nuclear gene sequences placed *L.* sp. B with its morphology-like species (*L. austromendocinus*) (Feltrin 2013; Medina et al. 2014, 2018) further supporting its possible hybrid origin. 2—Within the *L. lineomaculatus* section, *L.* sp. 4 is placed within the *L. somuncurae* clade with mtDNA gene tree, while the nuclear loci place it within the *L. kingii* clade (Breitman et al. 2011a, b, 2015). Its geographic distribution (Fig. 9.5, red stars) is between the distributions of the *L. somuncurae* clade (*L. somuncurae* and *L. uptoni*, Fig. 9.5, yellow dots), and the *L. kingii* clade species (Fig. 9.5, orange dots); thus a hybrid origin (similar to *L. parthenos* origin) or a possible mitochondrial capture event were hypothesized as possible processes for this interesting pattern (Fig. 9.11, pink stars). Last, although evidence is weak, a similar process may have been responsible for the origin of *L. abdalai*, for which the only sequenced individual (Fig. 9.11, 9-pointed yellow star) had a mtDNA haplotype within the *L. bibronii* complex (Martínez 2012), but its morphology places it in the *L. lemniscatus* species group.

An early second hint of introgression was suggested for species of the *L. fitzingerii* group in the Patagonian Steppe, for two areas of the Atlantic coastline (Avila et al. 2006; Fig. 9.10 yellow and blue circles with H, Fig. 9.11, pink circles along the coastline). Recent genomic evidence supported this hypothesis for the northernmost population (Grummer 2017), and added another probable area of hybridization in the easternmost boundary of the Somún Curá Plateau (Grummer et al. 2018; Fig. 9.10 orange circle with H; Fig. 9.11, northern inland pink circles). For this same group, Morando et al. (2009) detected some further introgression areas (Fig. 9.10 green circle with H, Fig. 9.11, southern inland three pink circles). These results were later corroborated in detail with genomic data, as *L. shehuen* X *L. melanops*, and *L. xanthoviridis* X *L. melanops* hybrid zones, and also with *L. fitzingerii* (Grummer 2017).

Another hybridization hypothesis in the northern Monte region of Patagonia (same area where hybridization was inferred for *L. darwnii-grosseorum*) was suggested for *L. bibronii* 8 X *L. gracilis* where these species are parapatrically distributed (Morando et al. 2007), and for which recent range expansions were inferred. Later detailed analyses of this zone provided the first solid evidence of hybridization between *Liolaemus* species (Olave et al. 2011, 2017). This study included two mitochondrial (cyt-b and 12S) and three nuclear gene regions and morphological data, and found six localities with asymmetrical *L. bibronii* X *L. gracilis* mtDNA introgression (Fig. 9.11, yellow circles). Olave et al. hypothesized that *L. gracilis* females may prefer the larger *L. bibronii* males in sympatry. Olave et al. (2018) developed a new coalescent method to detect hybridization in the presence of incomplete lineage sorting by evaluating the likelihood of different models with various levels of gene flow, and found strong statistical support for the *L. gracilis* female X *L. bibronii* male asymmetry hybridization in the empirical study.

The two *L. austromendocinus* clades separated by the Neuquén River have been recognized as *L. austromendocinus* Mza in the north (Fig. 9.4, red circles), and *L. austromendocinus* Nq in the south (Fig. 9.4, dark orange circles). Both have been hypothesized as candidate species based on morphological and niche model analyses (Feltrin 2013). The southernmost distribution of *L. austromendocinus* Nq

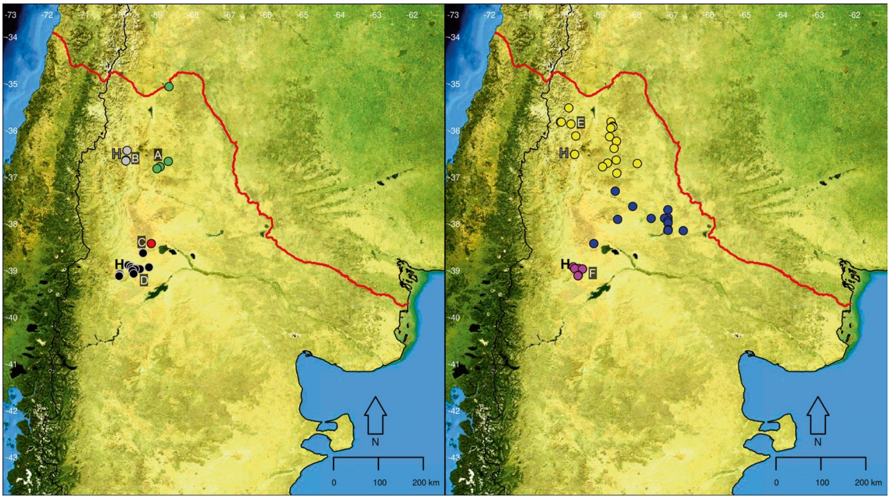

Fig. 9.12 Distribution area for the *Liolaemus donosobarrosi* species group based on phylogenetic and phylogeographic analyses. Letters represent type localities and colored circles mark georeferenced localities for each taxon A, *L. donosobarrosi*, green; B, *L. puelche*, grey; C, *L. calliston*, red; D, *L. mapuche*, black; E, *L. josei*, yellow; *L. cuyanus*, blue (type locality is outside Patagonia); F, *L. tiranti*, dark pink. Black "H" indicates area where these two species may be hybridizing, grey "H" slight evidence of hybridization between these two species (based on Avila et al. 2017)

overlaps with the northernmost distribution of the geographically limited *L. gununakuna* (Fig. 9.4, yellow circles), and individuals from this area (Fig. 9.4, letter "H") had *L. gununakuna* morphological characteristics but mitochondrial haplotypes closely related to *L. austromendocinus*_Nq. These data were interpreted as evidence of recent or past introgression (Fig. 9.11, yellow rhomboid) (Feltrin 2013).

The formal description of two new geographically limited *Liolaemus* species of the *L. donosobarrosi* group (Avila et al. 2017) (Fig. 9.12, grey "H") uncovered yet another possible case of introgression in *L. tiranti* (Fig. 9.12, pink pentagon). This sample had a mtDNA genome closely related to *L. mapuche*, whereas its nuclear sequences were closer to *L. josei*. Although further studies of this group are needed, available data suggest that the geographic location of this possible hybrid zone in northwestern Patagonia corresponds to the same region where other three cases of hybridization have been documented (Fig. 9.11).

Morando (2004) reported the karyotype of one individual of *L. rothi* (Fig. 9.11, pink square with an X) with 2/3 of the cells diploid ($2n = 34$), but 1/3 of the cells were triploid ($3n = 51$); this specimen was referred as a mosaic individual. Avila et al. (2006) detected mitochondrial haploclades of *L. rothi* intermixed with several lineages of the morphologically different *L. boulengeri* complex, which was hypothesized to include up to 10 allopatrically distributed species. This study system required detailed integrative analyses that Olave et al. (2018) addressed based on 2 mt and 12 nuclear genes, and morphological data from all species of these two complexes. A new "extra lineage contribution" statistic (XLC) was developed to explore the level of gene tree/species tree discordance, and this enabled testing of explicit hybridization hypotheses using coalescent model-based approaches. Olave et al. (2018) detected several instances of past (dated ~1 Ma) and recent hybridization between *L. rothi* and northern species of the *L. boulengeri* complex (*L. telsen*, *L. tehuelche*, *L. boulengeri*, Fig. 9.8, red circles with "H", grey circles showing the distribution of the *L. boulengeri* complex detailed on Fig. 9.9). Further, individuals with various levels of mixed ancestry were more closely related to *L. rothi* in terms of body size, but possessed a range of intermediate color patterns.

Yet another hint of hybridization was hypothesized by Breitman et al. (2015) that focused on the study of four species (*L. sarmientoi*, *L. escarchadosi*, *L. tari*, *L. baguali*) of the *L. kingii* clade (*L. lineomaculatus* section, Fig. 9.5), based on mtDNA, morphology and climatic niche modeling. Some individuals from parapatric areas had mixed morphological and mtDNA characters and their assignment was ambiguous, as they could be either *L. escarchadosi* or *L. tari*; also sympatric individuals of *L. sarmientoi* and *L. escarchadosi* were genetically assigned to one or the other species' main haploclades, but since there are no clear diagnostic characters, and they are morphologically variable and similar, more detailed genomic analyses are needed to further test hypothesis of species boundaries and putative hybridization among them.

In summary, for every *Liolaemus* group or complex studied from a phylogeographic perspective in Patagonian Steppe, evidence has shown various levels of introgression among closely as well as more distantly related species. Further, some hybridization appears to reflect historical events, while other cases are more recent and/or ongoing. Four species show some or strong evidence for a hybrid origin, one being the only parthenogenetic pleurodont, *L. parthenos*. Further, *L. parthenos* belongs to the *L. darwinii* group that includes oviparous and viviparous species, and several independent origins of viviparity and possible regressions to oviparity have been inferred within *Liolaemus* (King and Lee 2015; Esquerré et al. 2019a). Also, Chap. 10 summarizes a complex pattern of chromosome races within the single morphological species *L. monticola* in central Chile. The increasing number of publications suggesting cases of hybridization among *Liolaemus* species, including not only closely related species but also deeply divergent taxa, has led to consider hybridization a common phenomenon in these lizards (Olave et al. 2018). The role of hybridization in shaping the extraordinary diversity of the genus is still uncertain and deserves further study, given the increasing importance that hybridization processes have received to model rapid radiations (Kozak et al. 2015; Pease et al. 2016; Meier et al. 2017; Irisarri et al. 2018; Malinsky et al. 2018). As genomic data are generated for these lizards in future studies, we can "expect the unexpected"; for example, in the lacertoid lizard *Zootoca vivipara*, hybridization among individuals from oviparous and viviparous species give birth to viable individuals, however with lower fitness than pure parentals (Elmer 2019). The geo-climatic history of the region has been complex (summarized in Chaps. 3 and 4), with extensive tectonic uplift of the Andes, volcanism, multiple glaciation cycles, correlated with multiple shifts in sea levels (e.g., Ponce et al. 2011; Rabassa et al. 2011). All of these have generated an extremely heterogeneous geological evolution of the Patagonian landscape, which in turn has strongly influenced the evolution of the native Patagonian biota. For most of the introgressed lizard complexes, range expansions (demographically or geographically) have been inferred, which most probably repeatedly brought previously separated populations into contact and allowed interspecific gene flow. New methods to approach speciation with gene flow are being developed and most surely this genus offers very good candidate study models. Analyses of genomic data with these methods, along with dense population sampling, should clearly distinguish cases of hybridization from incomplete lineage sorting, the latter of which could also be extensive if diversification was relatively rapid (Olave et al. 2015).

The high prevalence of hybridization in this highly diverse genus may be related to its conserved generalized morphology that led to the pronouncement of "Jack of all trades and master of none" (Abdala et al. 2014). Generalist species are considered to have advantages in fluctuating environments, such as those that have occurred throughout the history of Patagonia, and there is evidence that *Liolaemus* may have persisted in several refugial areas (Sect. 9.7), with later expansions and radiations that allowed them to colonize different areas (e.g., Olave et al. 2015; Pincheira-Donoso et al. 2015). In this context, hybridization could be hypothesized as adaptive (e.g., Becker et al. 2019; Meier et al. 2017), either enabling the rapid increase of genetic variability after episodes of isolation/bottlenecks and/or by preventing specialization. These processes in turn may have played an important role in the lower extinction rates inferred for *Liolaemus* compared to its sister genus *Phymaturus* (Olave et al. 2020b). The *Liolaemus rothi* complex is characterized by morphological stasis among otherwise molecularly different species (Olave et al. 2017), and most probably similar patterns may characterize other *Liolaemus* complexes. New methodological approaches are needed in order to test these scenarios and clearly distinguish among alternative possible causes.

Within the genus *Phymaturus*, the *P. spurcus* group shows a complex polymorphic coloration pattern along with high mtDNA similarity among most of its geographically closely distributed species; some authors consider this complex a single species (see Sect. 9.1). Morando et al. (2013) noted that patterns of genetic variation observed for *P. excelsus*, *P. spectabilis*, and *P. spurcus* could also be interpreted as interspecies hybridization. All individuals from these species had almost identical mtDNA gene regions (cyt-b and 12S), but across the four nuclear loci (Phy89, Phy84, Phy38, PLRL) these species were distinguished by either fixed nucleotide differences, or were heterozygous in the same positions, and some individuals were heterozygous for gaps of large stretches of DNA. Nonetheless, considering the very different natural history characteristics of these two sister genera, a much lower hybridization level is expected within *Phymaturus*.

9.7 The Role of Earth Dynamics in Shaping Lizards' Evolutionary Histories

"If we accept Dobzhansky's view that evolution in essence means disturbance of equilibrium, we may see in the fact of the development of so many subspecies and species the evolutionary process in an especially plastic genus that is meeting the requirements of new environments", Hellmich (1951). Hellmich (*op. cit.*) was so surprised by the variability of characters between closely related species or within populations of *Liolaemus*, that he even defined new terms in an attempt to categorize different underlying influencing factors. He visualized two main factors affecting diversification of *Liolaemus*: (1) an ancient one, probably related to Andean orogeny, and (2) a specifically detailed model that related glaciation cycles and associated changes in temperatures, with lizards' expansions, in many cases from glacial refugia, and contractions, and subsequent dispersals concordant with the progression of aridity. He mentioned how some characters most probably were related to specific environmental conditions and considered hybridization as a possible contributing factor.

Recent biogeographic work on *Liolaemus* and its sister genus *Phymaturus*, based on several explicit methods, have inferred the Andes and in some cases also Patagonia, as their most possible ancestral areas (Díaz Gómez 2011; Portelli and Quinteros 2018; Esquerré et al. 2019a). Specifically, for *Phymaturus* Hibbard et al. (2018) inferred the ancestral area to be located over a relatively narrow strip following the Andes in Northwestern Patagonia up to ca. 33 °C, and a barrier at the middle of this ancestral range that most probably represents the split between the two main *Phymaturus* clades. Although they detected that most *Phymaturus* species are highly localized endemics, they found evidence to suggest that they must have been able to disperse southward to the Patagonian Steppe (*P. patagonicus* clade), as volcanic outcrops were available, and to the north (*Phymaturus palluma* clade). They proposed several dispersal, vicariance, and extinction events (Hibbard et al. 2018, their Fig. 8) that need to be tested when a strongly supported phylogenetic hypothesis became available, as these methods are dependent on tree topologies that still have many uncertainties (Fig. 9.1). Regardless of the limitations of still unresolved phylogenetic relationships within each of the genera, and the uncertainties on dating splitting events, both precluding inferences about more specific models of earlier diversifications linked to orographic events, there is a general agreement that the Andean dynamics had an important effect on the diversification patterns among the main Patagonian Liolaemini clades, since fossils have been recorded since the Early Miocene (Chap. 6) from the Patagonian Steppe. The recent biogeographic study of Esquerré et al. (2019a) demonstrated higher speciation rates in Andean species compared to lowland species, and inferred that the Andean orogeny acted as a "species pump" driving diversification of Liolaemini. However, Olave et al. (2020a) argues that this study fails in considering the heterogeneous diversification rates between *Liolaemus* and *Phymaturus*, and that ignoring such differences led to wrong conclusions. Specifically, *Phymaturus* displays approximately 3× higher speciation and extinction rates than *Liolaemus* (see Olave et al. 2020b), and given the fact that Esquerré et al. considered all *Phymaturus* species as "Andean", their results have confounded the extremely high general speciation rates for the genus, with a single "Andean uplift" response. Olave et al. (2020a) re-analyzed the data of Esquerré et al. and did not find a *Phymaturus* "Andean uplift" signal when accounting for the diversification shifts when they included novel "hidden states" models in the analyses. Further, Olave et al. (2020a) found that changes in global temperature better explain changes in *Phymaturus* speciation rates, in agreement with results presented in Chap. 13.

Another major factor that most surely had a role in more recent diversification dynamics in Patagonia were glaciation cycles that occurred intermittently over the past 7–5 Ma (Rabassa 2008; Chap. 4). These events affected physiognomy, wind patterns, temperatures, sea levels river basins, and humidity/aridity levels (e.g., Markgraf et al. 1995; Moreno 1997; Chaps. 3 and 4); consequently, they impacted all of the biota. Particularly during Quaternary deglaciation periods, river basins were enlarged at different times (Martínez and Coronato 2008; Martínez and Kutschker 2011; Chap. 4), and given that several phylogeographic breaks have been associated with them, most probably they promoted isolation between populations of many species. Historically, the Deseado River (ca. 47° S) was an important drainage (Martínez and Coronato 2008), and it has been inferred as a main barrier for lizards (Breitman et al. 2015; Morando et al. 2007), plants (Sede et al. 2012; Cosacov et al. 2012; Nicola et al. 2014, 2019), and rodents (Kim et al. 1998). Further, other rivers including the Chubut, Chico, Coig, Neuquén, and Colorado have been hypothesized as possible gene-flow barriers for lizards (e.g., Morando et al. 2003, 2007; Breitman et al. 2012, 2013), plants (Cosacov et al. 2012; Baranzelli et al. 2018; Nicola et al. 2019), and rodents (Lessa et al. 2010). As detailed phylogeographic analyses continue to increase, it will soon be possible to integrate these datasets with paleo-distribution models and more precise divergences estimates, to specifically test levels of spatio-temporal congruence of these breaks, and estimate the relative impact of paleo-basins on the diversification of regional biotas.

Further associated with glaciation cycles, several congruent patterns of post-glacial dispersals and populations' expansions from putative refugia (most of them based on plants) have been hypothesized, some mentioned in the above sections. Although spatio-temporal concordance studies among taxa is lacking, a spatio-temporal model has been applied for *L. darwinii* (Camargo et al. 2013), and a detailed time-calibrated model in agreement with recent glacial/interglacial cycles (~85 ka, 55 ka, 21 ka), depicting a mainly southeastern expansion in Monte region in northern Patagonia, has been proposed. A similar model was recently proposed for a southern Patagonian plant species (Baranzelli et al. 2018), and its pattern is congruent with general observations of lizards in the same region (Breitman et al. 2012). This approach shows promise but still remains largely unexplored.

In the above context, we briefly summarize general qualitative patterns in several clades of lizards that need further detailed comparative studies. Hypotheses of refugial areas include: (1) a highly fragmented area in northwestern Patagonia for almost all species distributed in that area; (2) central and southwestern periglacial "free of ice pockets" regions for species in the *L. lineomaculatus* section; and (3) eastern "now-below-sea level" land areas, with narrow strips of the present coastline occupied by species of the *L. fitzingerii* group and *L. lineomaculatus* section. Concomitantly, proposed expansion routes are from northwestern Patagonia toward the southeast (*L. darwinii*, *L. bibronii*, *Aurivela longicauda*), and southwest (*L. elongatus*, *L. kriegi*, *L. lineomaculatus*, *L. rothi*), from central and southwestern periglacial refugia to the east and south (*L. lineomaculatus* section), and from the eastern territories to the west and south (*L. fitzingerii* group, *L. lineomaculatus* section and *L. bibronii*). A particularly interesting area in northwestern Patagonia is the Auca Mahuida–Auca Mahuevo region, where in 1997 the first dinosaur eggs with embryonic remains were found (Dingus et al. 2000; Chiappe et al. 1998, 2000, 2001). Almost every lizard species found there is an endemic, and virtually all are also characterized by high genetic variability.

The complex geomorphological and climatic history of the Patagonian region continually provided new changing environments and multiple instances of isolation. Considering the natural history characteristics of the species-rich genus *Liolaemus*, most probably its evolutionary history is a colorful and challenging mosaic history that reflects a combination of geographic, geological, and climatic influences (Simões et al. 2016). This history would present multiple allopatric speciation opportunities, coupled with components for intra-group adaptive radiations, and a decrease in extinction rates through time (Olave et al. 2020b). The interplay between extrinsic environmental factors with genetically based morphological characteristics, and sexual and natural selection in light of multiple instances of hybridization (i.e., speciation versus degrees of reproductive isolation), surely will be a fascinating and productive new line of research. Comparisons with its highly distinct sister genus *Phymaturus* will lift the Liolaemini clade to the level of a world-class model to test many macroevolutionary questions (Pincheira-Donoso et al. 2015; Wollenberg Valero et al. 2019; Olave et al. 2020b).

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Chapter 10
Phylogeography of Chilean Lizards: Histories of Genetic Diversification on the Western Slope of Southern Andes

Pedro F. Victoriano

Abstract The western slope of the Southern Andes has complex orographic attributes and a dynamic paleoclimatic history, which seems to have been the driver of a great intraspecific genealogical diversification of lizards. Phylogeography tries to explain the spatial current patterns of genetic variation and genealogical intraspecific diversity, alluding to the features and the history of geographical scenarios. Although the number of these studies for South America is still low, the contributions that have emerged in recent years about the intraspecific diversification of reptiles in Chile have begun to sketch interesting hypotheses about the geographical factors that have likely contributed to the distribution of their genetic diversity. Such studies have focused mainly on species of the genus *Liolaemus*, the one with the highest levels of squamate species richness in southern South America. In West Austral Andes, a large part of the herpetofaunal diversity is concentrated in the Mediterranean and northern areas of the temperate forest, where several species are characterized by wide geographical ranges across varied environmental conditions. The general evidence indicates that the Chilean lizards have acquired high levels of genetic variability, coupled with complex geographic distributions and high levels of evolutionary differentiation, associated with landscape features, such as rivers and mountains. These influences have been further impacted by the interaction with dramatic past climate changes. Estimates based on mtDNA suggest that some of the species diversified during the Pleistocene (e.g., *L. tenuis* and *L. pictus*). These species have likely been most impacted by glaciations, suggested by a greater number of population reductions and postglacial expansions at greater latitude and altitude. These and other species, however, also show considerable levels of divergence and the existence of cryptic diversity (e.g., *L. tenuis*, *L. pictus,* and *L. monticola*). These patterns suggest that there may be more than one species within those that until now have been considered single taxonomic entities. It is also interesting to detect cases

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P. F. Victoriano (✉)
Laboratorio de Microevolución y Ecología de Vertebrados (MEV),
Departamento de Zoología, Facultad de Ciencias Naturales y Oceanográficas,
Universidad de Concepción, Concepción, Chile

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of congruent diversification among co-distributed lizards. From a biodiversity conservation perspective, the allopatric distribution of lineages of deep divergence and the spatial arrangements of genetic diversity and singularity suggest the existence of valuable intraspecific conservation units, most of which would be unprotected and in areas exposed to important anthropogenic changes.

Keywords *Liolaemus* · Intraspecific conservation · Southern Andes · Population differentiation

10.1 The Phylogeographic Context and Lizards

Knowing the spatial arrangement of genetic diversity and understanding the geographic processes that have influenced its evolutionary dynamics is relevant for two main reasons. On the one hand, inquiring about the environmental factors that have influenced the genetic diversification within a species is a key issue in evolutionary biology, in order to understand, among other aspects, the mechanisms that prelude speciation events (interface between micro- and macroevolution). And on the other hand, intraspecific variation constitutes a real component of biodiversity, and its study when taken to the geographical context is fundamental to define the intrinsic conservation value of evolutionary units within species (Moritz 2002). This is also a necessary aspect to predict the negative consequences on the number and spatial distribution of intraspecific lineages that the alarming global changes in course will bring.

At the end of the 1980s, when population genetics and phylogenetics were already mature disciplines, Avise and collaborators proposed creatively merging both approaches to better understand the evolution of populations within the framework of the attributes of the geographical landscape (Avise et al. 1987). They took advantage of the synergism between both disciplines and coined the term phylogeography to refer to the study of the principles and processes that have influenced the geographical distribution of lineages, especially those within species (Avise and Walker 1998). Their contributions come from studying the distribution of genetic biodiversity, including the reconstruction of genealogies, to explain their origin and distribution based on the history of the geographical space (Fig. 10.1). In a certain way, it can be said that biogeography and phylogeography, having common interests, just differ fundamentally in their temporal scales and in the hierarchies of the biodiversity they address. In its performance, phylogeography also calls for other disciplines, such as population ecology, paleontology, molecular biology, and geology, among others, allowing an integrated interpretation of the processes that affected the diversification of populations. In this way, phylogeography interacts and generates complementary contributions with other disciplines, such as genetic ecology (Lowe et al. 2004) and landscape genetics (Manel et al. 2003). Phylogeography contributes with evidence and methods to other disciplines too.

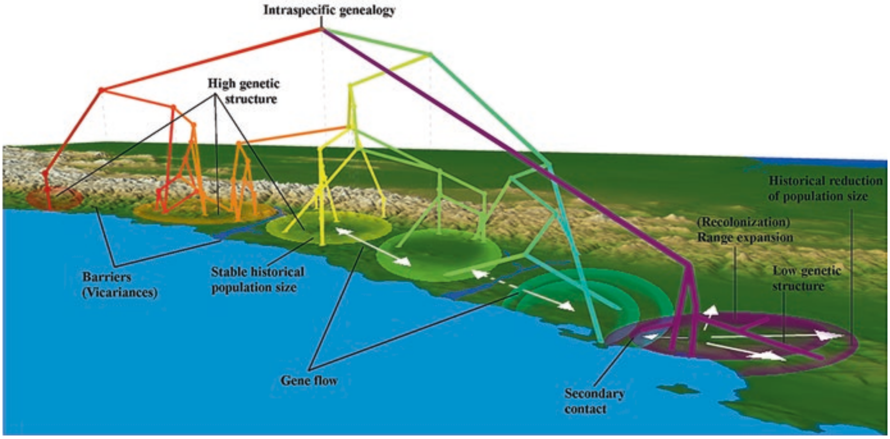

Fig. 10.1 Intraspecific hypothetical genealogy projected on the geographical landscape and some of the patterns and processes analyzed in phylogeographic studies

The terms geogenomics and phylogeology were recently proposed as new subdisciplines of geology that integrate geologically relevant genetic evidence on a large scale, to test geological hypotheses (Acosta et al. 2014; Baker et al. 2014; Fritz and Baker 2017). In summary, phylogeography provides a great real and potential contribution to the knowledge of the history of Earth and in turn how and why populations have evolutionarily differentiated.

Despite the complexity of evaluating the role of spatial and temporal variations in the environment as promoters of intraspecific differentiation (Hewitt and Ibrahim 2001), two aspects are recurrent in the phylogeographic literature. On the one hand, the historical stability of habitat, understood as the degree of historical persistence of environmental conditions, seems to be an important factor for the herpetofauna, both at the intraspecific (e.g., Carnaval et al. 2009) and multispecies or community level (Werneck et al. 2012). On the other hand, the historical discontinuity of the habitat, with repercussions on population connectivity, would have functioned as an important diversification force (e.g., Bell et al. 2010). The interaction of both aspects would have influenced the formation of the spatial arrangements of the current genetic diversity, with responses dependent on the biology of each species (e.g., vagility, age of taxa, reproductive attributes, requirements, and tolerances). In this context, phylogeographic evidence suggests that areas that have long maintained their environmental conditions (e.g., climate and vegetation structure) have tended to harbor greater genetic variability and higher demographic stability, compared to scenarios that have drastically changed throughout time. In the case of habitats broken up by barriers, sometimes as archipelagos with small "islands," these have contributed to population reduction events due to environmental change and should promote greater genetic differences between populations (structuring), with lower local diversity. In this sense, species of lizards that for a long time have existed along wide geographic ranges, with an interrupted geography and with different degrees of stability, should harbor complex spatial patterns of genetic diversification. This is the case of several species distributed in central-southern Chile, which is a territory with a high orographic heterogeneity and subjected to the effects of repeated glaciations (Heusser 2003).

Camargo et al. (2010) made an excellent review on the suitability of lizards as model species in evolutionary studies, given the knowledge about demographic aspects, life histories, and ecophysiology, among others. Although there are still considerably fewer phylogeographic studies for the Southern Hemisphere, they have increased since the 2000s (Beheregaray 2008), where herpetozoans are in an intermediate ranking, below mammals and plants, but above aquatic invertebrates and birds. In an interesting phylogeographic review of South America, Turchetto-Zolet et al. (2012) concluded that the herpetofauna includes species of old intraspecific divergences and with varied responses to glacial cycles, depending, for example, on the type of habitat (e.g., open or wooded). In this study, it is also clear that mitochondrial genes have been used in the majority of cases, and a smaller number of studies have included multilocus approaches. Recently, there have been works that incorporate NGS methods (massive parallel sequencing), although for lizards these still address phylogenetic relationships among multiple species, and the analysis in a phylogeographic context is still pending. For example, Panzera et al. (2017) recently published a phylogeny of *Liolaemus* species of the Chilean clade based on ultraconserved elements (UCEs), while Grummer et al. (2018) used a genomic approach for Patagonian species of the *Liolaemus fitzingerii* group. Although in Chile the greatest richness of lizard species extends from 23° S, in desert environments in the north, to 39° S in parts of the temperate forests in the south (Vidal et al. 2009; Vidal and Díaz-Páez 2012), a considerable diversity is concentrated in Mediterranean environments (Troncoso 2010). The total lizard richness in Chile comprises approximately 130 species, of which about 50% are endemic (Vidal and Díaz-Páez 2012) and 68 species are threatened (http://www.mma.gob.cl/clasificacionespecies/index.htm). The greatest lizard diversity of this part of South America is represented by species of the genus *Liolaemus*, an ecologically versatile and evolutionarily prolific group. Although still scarce, the phylogeographic literature suggests a complex and interesting history of diversification for these lizards. The objective of this chapter is to give a general view about the patterns and processes of intraspecific evolutionary diversification of lizards from central-southern Chile, based on the phylogeographic information published up to now, and to give some guidelines for future investigations in this field.

10.2 The Chilean Scenario

The Andes mountain range, which extends for more than 7000 km, constitutes the longest mountain chain on the planet (Ceccarelli et al. 2016). Although its beginnings go back to the Paleozoic (Ramos and Alemán 2000), its uplift would have been accentuated approximately 23 Ma, reaching a relief with heights similar to the current ones about 5 Ma. The extravagant and singular geography of central-southern Chile extends on the western slope of the Southern Andes (approx. 30° S–43° S), forming part of the Mediterranean Province from Santiago to the rainy Valdivian Forest, according to Morrone (2015). This part of South America has been a scenario with important evolutionary repercussions on its biota (Sérsic et al. 2011), where, compared to other mountain systems of the world, the role of physical factors such as temperature, rainfall, and relief seems to have been the most relevant in the processes of biological diversification (Antonelli et al. 2018). The most obvious effect was the East-West divide, which would have led to a marked differentiation between the biota of its Pacific slope and that of Argentine Patagonia, and in part was one of the mechanisms that generated the endemism in what is known as the Chilean hot spot of biodiversity (Myers et al. 2000). In the west, a series of latitudinally arranged basins added numerous interrupted areas, also distributed along a pronounced climatic gradient, and are being able to promote transverse speciation processes as found by Wallis et al. (2016) in the Alpine range. This arrangement of speciation could be one of the responsible factors for latitudinal endemism and a high phylogeographic differentiation within the western slope of the Southern Andes. For these reasons, central-southern Chile constitutes a privileged scenario to test phylogeographic hypotheses, with attributes of a great natural laboratory.

10.2.1 Chilean Physiography and Climatic Gradients

Although it is not reasonable to refer to the phylogeographic space in geopolitical terms, in the case of Chile it is a minor problem, due to the high concordance between its territorial limits and its natural barriers. Its physical attributes facilitate in some way the prediction of expected phylogeographic patterns and the proposal of hypotheses about their causes. The main physiographic units of central-southern Chile are the Cordillera de la Costa, close to the Pacific Ocean, and the Cordillera de los Andes, both mountainous systems oriented latitudinally in a parallel arrangement and unconnected along a large part of their distributions. The intermediate depression or inner valley is located between these two mountain ranges, which forms an almost continuous flat area between 34° 30′ S and 37° 30′ S (Fig. 10.2a). This is a narrow scenario arranged vertically on the map, with a marked isolation imposed by the Andes to the east, the Pacific Ocean to the west and south, and the desert to the north. The Chilean relief shows interesting altitudinal gradients, both longitudinally (from the Andes to the Pacific coast) and latitudinally (Fig. 10.2b). For example, at the latitude of Santiago (33° S), mountains that exceed 4000 m are frequent, and valleys are often interrupted by transverse ranges that connect the Andes with the coastal mountain range. Toward the south, the mountains decrease in altitude, increasing the connectivity between low-altitude environments. Consistent with this geographical trend, the Andes gradually weakens as a barrier toward the south, which would have allowed greater historical communication between populations of the Patagonian and Pacific slopes. There is phylogeographic

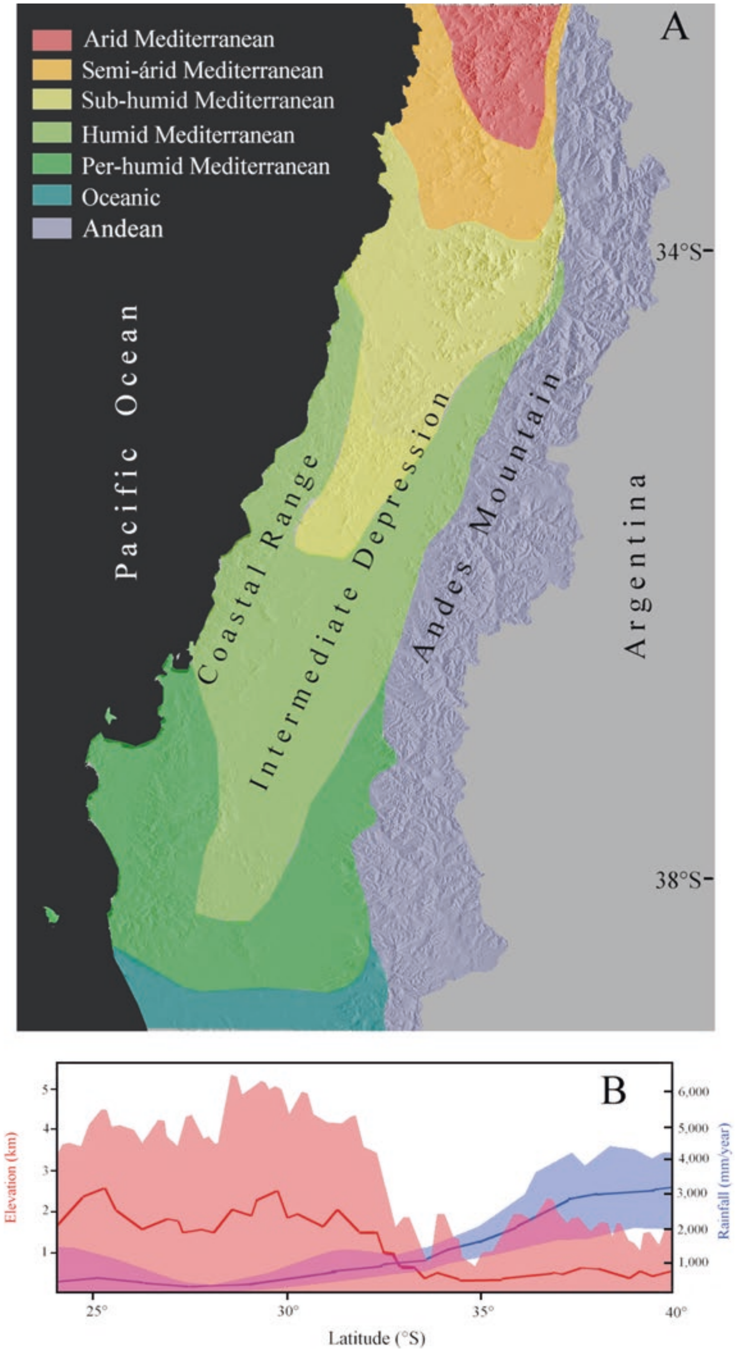

Fig. 10.2 (**a**) Major bioclimatic zones of Chile (based on Di Castri 1968). (**b**) Swath profiles showing rainfall and topography in west Southern Andes (based on Strecker et al. 2007)

evidence for this, as is the case of some freshwater fish (Muñoz-Ramírez et al. 2014; Ruzzante et al. 2006). This is also consistent with the presence of lizard species shared between Chile and Argentina south of 38° S, such as *Liolaemus tenuis, L. lemniscatus, L. pictus,* and *L. cyanogaster*.

Various bioclimatic classifications have been proposed for Chile, although in general they all describe categories of a latitudinal climatic gradient (e.g., Kuschel 1960). For example, Di Castri (1968) subdivided the zones of moderate altitude of the geographic range where most of the species of this chapter are distributed into a series of ecoregions of increasing humidity and cold toward the south (Fig. 10.2a, b), a pattern generated in part by the prevailing winds that bring moisture from the Pacific Ocean. This area ranges from the arid Mediterranean to the north (with a southern limit near 33° S), passing through the subhumid (34° S to 36° S), to the Oceanic which starts from 39° S southward in Araucanía. At this last latitude, there is a marked break in the climatic conditions, which is the limit between the mesomorphic zone (mainly Mediterranean) and the hydromorphic forested, humid, and cold zone. To the East, and throughout all the previous zones, the high Andean ecoregion is located.

10.2.2 Past Climate Changes and Predicted Phylogeographic Patterns

Southern South America has been exposed to recurrent climatic changes in the past (Heusser 2003), which caused important changes in the geographic distribution of the biota (Turchetto-Zolet et al. 2012; Ruzzante et al. 2008). In this part of the Earth, glaciations occurred since the end of the Miocene, approximately 6 Ma, with an accentuated effect on the Andean relief during the Pleistocene, for about 1 million years, with the Great Patagonian Glaciation (Rabassa et al. 2011). Associating the glacial dynamics with the relief and latitude in Chile, the effects of past climate changes were of greater intensity in the mountainous heights and of greater extension toward the south, where they affected lower areas too (Fig. 10.3a, b).

According to this, it is reasonable to predict the detection of signals of greater demographic and distributional changes at higher latitudes. Although phylogeographic processes should be understood as accumulated phenomena along multiple glaciations (Klicka and Zink 1997), the most cited event is the most recent, the Last Glacial Maximum (LGM). This occurred approximately 23,000–18,000 years ago (Hulton et al. 2002) and modified the landscapes throughout the entire temperate forest distribution of the Southern Andes due to the presence of an ice shield that extended from 36° S to 56° S. Although marginally, it extended northward between 38° S and 34° S, following the heights of the Andes mountain range (Hollin and Schilling 1981; Heusser 2003). During LGM, the sea level dropped by 130 m (Fig. 10.3c), connecting the islands near the coast with the mainland. This would have allowed some species to temporarily colonize habitats that subsequently

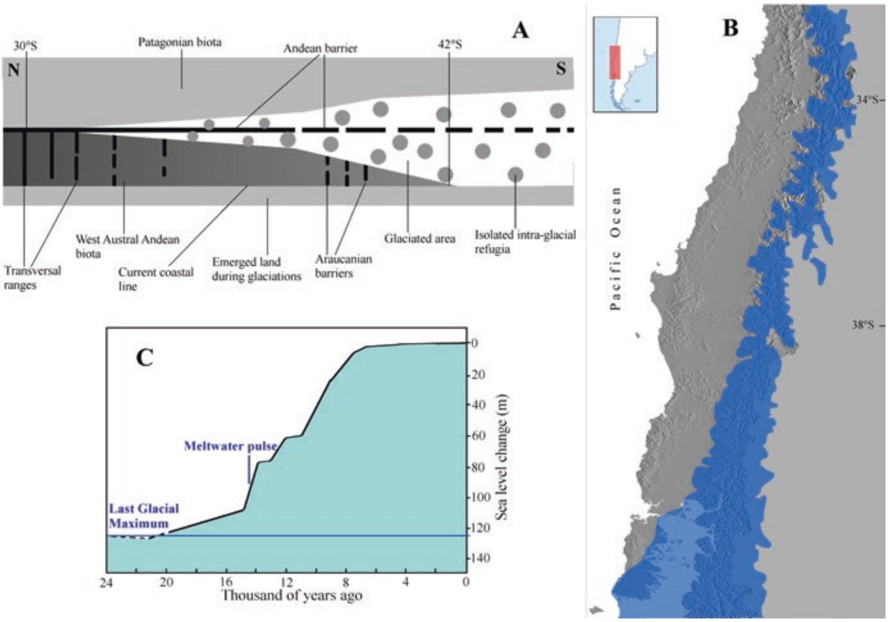

Fig. 10.3 (**a**) Generalized model for south-central Chile, showing geographic and paleoclimatic attributes of phylogeographic importance. (**b**) Last Glacial Maximum (LGM) extension in central-southern Chile. (**c**) Variation of the sea level from the LGM to the present (based on Fleming et al. 1998)

disappeared again during the interglacial phases. During each glacial event, the forest and its associated fauna would have been displaced from their higher ranges and expanded to the north and to lower altitudes (e.g., *Austrocedrus chilensis*; Souto et al. 2015), caused by higher humidity and lower temperatures (Villagrán et al. 1995). The glaciers probably reached sea level south of the Piuchén Mountain Range on the island of Chiloé (approx. 42° S), thus extending to the southern tip of South America (Fig. 10.3b, Chap. 4). Although relatively continuous, this glacial shield would have sheltered small ice-free refugia, inserted onto an icy matrix, in small Andean valleys and active volcanic zones. In these “ice-free islands,” there would have persisted populations that later functioned as sources of recolonization, once the ice retreated. For example, both the Ñuble’s Andean zone (37° S) and the Lonquimay Valley (38° S), in Chile, probably remained free of ice (Vera-Escalona et al. 2012). The occurrence of intraglacial refugia (probably many were cryptic refugia) could explain the current patterns of genetic variation in some organisms such as trees, lizards, freshwater crabs, and amphibians, among others (Xu et al. 2009; Nuñez et al. 2011). In a phylogeographic review, Sérsic et al. (2011) proposed hypotheses on refugia and probable routes of dispersion, both for Patagonia and for the Chilean slope. For example, and mainly for plants, they proposed the existence of refugia near the Pacific coast, including the Cordillera de la Costa, north of 42° S. In summary, the phylogeographic consequences of the glacial phases on the biota of the western slope of the Southern Andes seem to include (1) fragmentation and reduction of effective population sizes during the presence of ice shields, with a gradually greater effect toward greater latitudes, and (2) expansions subsequent to the glaciations, also with stronger signals at higher latitudes. An opposite pattern should be evidenced for the less affected populations of Central Chile, mainly along the Pacific coast. These areas would have been relatively stable (Villagrán 1991; Villagrán et al. 1995; Markgraf et al. 1995), for which we should expect clearer signs of historical demographic equilibrium.

10.3 Genetic Patterns and Phylogeographic Processes in Chilean Lizards

According to the underrepresentation of South American phylogeographic studies in comparison to what has been done for the Northern Hemisphere, the lizards of Chile have been seldom studied in this regard (Turchetto-Zolet et al. 2012). Even adding the phylogeographies of the other Chilean herpetozoa, such studies are scarce. For example, for snakes there is only one work in *Philodryas chamissonis* (Sallaberry-Pincheira et al. 2011), and for amphibians a few others (e.g., Vásquez et al. 2013; Victoriano et al. 2015).

For Chilean lizards, such works have mainly considered species of the genus *Liolaemus*, especially for those species distributed in the center-south areas of the country. Although restricted to this latitudinal range, these species have the virtue of covering a varied range of geographical scenarios (Fig. 10.4). For the other ten genera present in Chile (Vidal and Díaz-Páez 2012), there are only a couple of works on *Microlophus* species, predominantly distributed in coastal environments of the northern desert.

10.3.1 Intraspecific Evolution of Chilean **Liolaemus**

Liolaemus is the genus with the greatest number of species in the south of South America, and for which a high rate of new species descriptions continues, suggesting that its real diversity is still far from being well known (Abdala and Quinteros 2014; Avila 2010; Chap. 9). The recent description of several species of the genus on the western slope suggests that this trend will continue (Esquerré et al. 2013; Troncoso-Palacios et al. 2015, 2016, 2018). Similarly, a considerable number of species have been described on the Argentinean side, including cryptic diversity (e.g., Abdala et al. 2015; Avila et al. 2004; Medina et al. 2014; Morando et al. 2003; Olave et al. 2017). With more than 250 species, this genus is distributed from the central coast of Peru to the south, through Bolivia, Paraguay, Chile, and Argentina, reaching southward to Tierra del Fuego. At the East, it reaches the Atlantic coast of

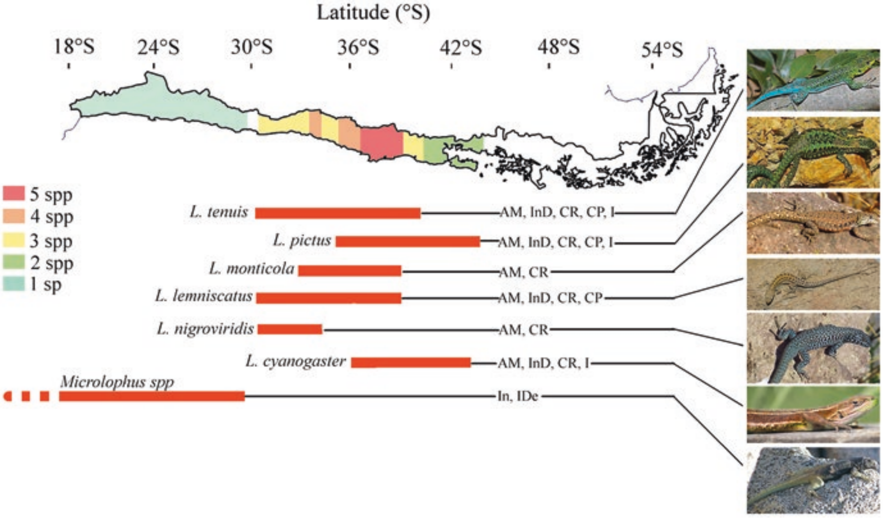

Fig. 10.4 Summary graph detailing the species or species groups analyzed in phylogeographic studies in Chile. The horizontal bars represent the latitudinal distribution. Presence in different physiographic units are indicated by acronyms: *AM* Andean mountain, *InD* Intermediate Depression, *IDe* Inner desert, *CR* Coastal Range, *CP* Coastal plains, *In* intertidal, *I* islands. Color scale corresponds to the number of studied species according to latitude in the map. Photo credits: *L. cyanogaster* (Jorge Álava), *L. monticola* and *L. nigroviridis* (Carlos Garín)

Uruguay and the southeast of Brazil (Etheridge and Espinoza 2000). Its great taxonomic diversity and wide geographic distribution, through topographically and climatically diverse landscapes, is accompanied by a remarkable ecological versatility. Some species inhabit rocky or sandy environments, others are present in wooded or scrubland environments, and others are typical of open steppes such as Patagonia (Díaz-Gómez and Lobo 2006). In some widely distributed species, as is the case of some in central-southern Chile, their populations occupy very contrasting environments and gradients (e.g., arid Mediterranean to humid Oceanic). Their evident tendency to diversification, adaptation to diverse environments, moderate vagility, and condition of ectothermic organisms especially sensitive to physical environmental conditions make these lizards good models for phylogeographic studies (see Camargo et al. 2010; Wollenberg et al. 2019).

Liolaemus seems to have had an Andean-Patagonian origin (Díaz-Gómez and Lobo 2006; Vidal and Díaz-Páez 2012). Among the visionary classic herpetologists, Hellmich (1951) had already suggested that the current diversity and distribution would be a consequence of expansions and contractions of older distributions, associated with the glacial and interglacial processes during the Tertiary. The Andes as a promoter of basal divergences in *Liolaemus* is already present in the proposal of Laurent (1983), who subdivided it into two subgenera, according to the distribution of this great geographical barrier: one corresponding to *Eulaemus* or the species present on the Argentine side and the other to *Liolaemus* or western group. However, the diversification of these two groups should not be oversimplified by association with a single vicariant event generated by the Andes. For example, molecular evidence suggests that the origin of viviparity in *Liolaemus* would have occurred several times mediated by a complex of vicariant and dispersion events, some even prior to the definitive uplift of the Andes (Schulte et al. 2000; Schulte and Moreno-Roark 2010). This intricate process of diversification could explain the occurrence in the south of a *Liolaemus* distribution that does not "respect" the Andean vicariance, erasing the reciprocal monophyly between the two sides of the mountain range. Recent estimates based on the molecular clock for the *Eulaemus* group suggest that the beginning of the diversification of this clade would have occurred approximately 19 Ma, and several of the divergences between sister species would be about 5 million years (Fontanella et al. 2012). According to preliminary estimates for pairs of Chilean species, the divergence of *L. lemniscatus*-*L. tenuis* would have occurred approximately 3.7 Ma (Vera-Escalona, unpublished data). The genetic diversity of some Chilean species would be about 2 million years old (Muñoz-Mendoza et al. 2017; Vera-Escalona et al. 2012). This indicates that the phylogeographic processes to which the *Liolaemus* species have been exposed would have covered a large part of the Pleistocene climate changes on an extremely heterogeneous geographical scenario. Phylogeographic studies tend to mainly consider recent glacial events, such as LGM as a causal factor of diversification, probably because traces in the genome are also more evident for younger processes (Late Pleistocene Origins model, LPO). However, such consequences should be interpreted in light of the summed effects of several older glacial processes (Klicka and Zink 1997). The evidence gathered so far for the Chilean *Liolaemus* suggests trends largely consistent with the physical and paleoclimatic attributes of the western slope of the Southern Andes. Their patterns are characterized by high levels of genetic diversity, with an accentuated structure, often detectable in small geographic ranges, and with evidence of contrasting demographic processes according to latitude and altitude. In some cases, the magnitude of the divergences also suggests the existence of cryptic diversity, probably cases of species that have not yet been delimited.

10.3.2 Lizards Evolving Within Mountains

An interesting case of *Liolaemus* species that have evolved in close association with mountainous ecosystems is the *monticola* group. These saxicolous species characterized by a dark coloration, probably as a result of adaptations to Andean basaltic environments, are found above 1000 m, between 30° S and 40° S. In the case of the species *L. monticola*, some of its populations at the latitude of Santiago (approx. 33° S) are connected to the Coastal Range due to the existence of transverse ranges at that latitude, where the elevated terrain would have worked as corridors. Because of its distribution, this species complex probably diversified under the effects of extreme relief conditions and, due to its altitude, probably under important effects of glaciations and volcanism. In fact, some of its species are closely associated with volcanic systems, such as *L. chillanensis* and *L. villarricensis*. During times of allozyme and karyotype methodology, the first works with some phylogeographic hypotheses for this group were already emerging in the 80s and 90s. More recently, Lamborot et al. (2003, 2012) found interesting patterns of differentiation of chromosomal races in *L. monticola*, associated with Andean fluvial barriers (Aconcagua and Maipo Rivers in Central Chile, approx. 33° S), with low rates of introgression. Some of these studies revealed an interesting geographic variation at the chromosomal level, in some cases with morphological agreement and with considerable levels of evolutionary divergence (Lamborot 1993, 1998; Lamborot et al. 1981; Lamborot and Alvarez-Sarret 1993; Lamborot and Eaton 1992, 1997; Lamborot and Vásquez 1998). For example, Lamborot et al. (1981) found differences in the fundamental number of chromosomes between the previously considered subspecies of *L. monticola* (*L. m. monticola, L. m. chillanensis,* and *L. m. villarricensis*), allowing to distinguish between the nominal subspecies and the other two distributed in the south. Genetic variability based on allozymes for two syntopic morphs from the Chillán volcano (*chillanensis* and *Liolaemus* sp.) evidenced absence of gene flow between both, which also differ in an attribute of high constancy in the genus as is the presence of precloacal pores in males. This served as motivation to suggest they represented two co-distributed cryptic species (Torres-Pérez et al. 2003). Integrating genetic and morphological evidence, the hypothesis that the subspecies involved cryptic diversity at the level of different species was strengthened. It was also established that these do not conform a natural group but polyphyletic (Torres-Pérez et al. 2009, 2017). This suggests evolutionary processes that led such unrelated species to converge similar phenotypic traits, probably conditioned by common environments. For these species, one of the components that has generated geographic discontinuity in the Andes has been the presence of rivers that could have functioned as barriers for a long time and have promoted differentiation (Lamborot and Eaton 1992). Vásquez et al. (2007) added alloenzymatic evidence that reinforced the idea that morphological and genetic differentiation in *L. monticola* was mediated by the action of fluvial systems, and Torres-Péres et al. (2007) suggest that the action of fluvial barriers for this group of *Liolaemus* would have been key in its diversification over a prolonged time. Other groups of mountain lizards of Chile could fit into this model and have not yet been analyzed in a phylogeographic context, as is the case of several species of *Phymaturus* distributed in the intricate Andes between 25° S and 45° S. Seven of the nine species have been described for Chile during the 2000s, and several of them after 2010 (Núñez et al. 2010; Pincheira-Donoso 2004; Troncoso-Palacios and Lobo 2012). A comprehensive recent study has revealed for this genus the existence of great diversity not previously described (Morando et al. 2013) and, although widely distributed in Patagonia, several of its species would have been generated in intra-Andean scenarios. Another case of lizards that would have evolved in montane environments is that of *L. nigroviridis*, a saxicolous species from Central Chile (30° S to 34° S). Although three subspecies were proposed

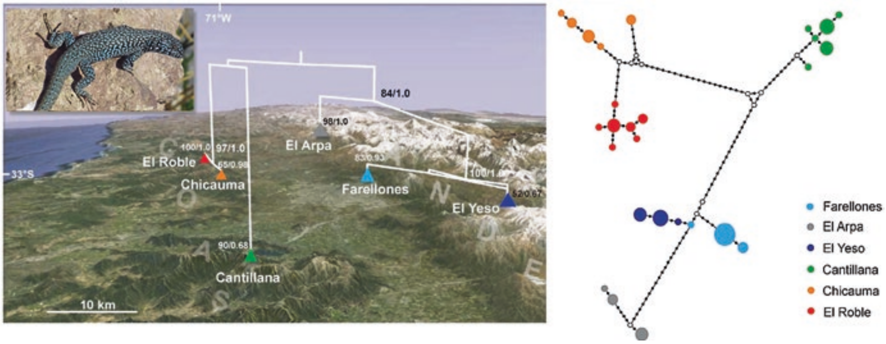

Fig. 10.5 Phylogenetic tree and haplotype network of the Andean species *Liolaemus nigroviridis* (adapted from Cianferoni et al. 2013. Photo of *L. nigroviridis* by Carlos Garín)

for this species in the 30s to 60s based on their allopatric distribution and putative morphological differences, these were not later evidenced by morphological and karyotypic analyses, leaving *L. nigroviridis* as monotypic (Núñez and Jaksic 1992; Valencia et al. 1979). A recent phylogeographic study based on mitochondrial DNA showed an important evolutionary divergence between populations of Andean habitats and those of the Coastal Range, at the same latitude (Fig. 10.5), which would have occurred approximately 2.7 Ma (Cianferoni et al. 2013).

The interesting thing about their diversification processes is that they would have occurred according to a dynamic of isolated high-altitude environments (“Sky Islands”), where the valleys would have functioned as barriers most of the time. The permeability of such valley barriers probably varied according to the glacial cycles (greater connectivity for this species in low areas during each glaciation), allowing at those stages the exchange between coastal and Andean populations. However, this explanation should be reconsidered after taking into account mtDNA information from a dense geographic sampling. A molecular study that included other species of the genus, revealed *L. nigroviridis* could be polyphyletic (Torres-Pérez et al. 2017). In summary, lizards restricted to high altitude in the Andes are a good model for the study of phylogeographic diversification and speciation in montane environments, which may have been due to prolonged processes of isolation and environmental instability. It also seems frequent that in these scenarios species would have originated in restricted geographical areas within an extremely discontinuous landscape. The great degree of geodiversity of the Andes, its numerous rivers, and the complex spatial distribution of the glacial effects had to play an important role in the processes of diversification of lizards. In this sense, the Andes has not only generated strong vicariant effects resulting in the Eastern Patagonian lizards and the Chilean group in the Pacific slope, but it has been a prolific scenario of in situ diversification, functioning as a true “species pump” (Sedano and Burns 2010).

10.3.3 Diversification Throughout Gradients, Barriers, and Glaciations

Long-standing gradient scenarios offer certain advantages in evolutionary studies because, by generating different selection pressures and gradual magnitudes of gene drift, they can, for example, promote parapatric diversification (Losos 2009). Environmental gradients have been highlighted as modulators of species richness and with complex synergies between topography, climate, and vegetation (Moura 2016). Few species of lizards offer the advantage of a wide distribution west of the Andes, as is the case of *L. tenuis*. This makes it a good model to understand how environmental forces have acted in processes of intraspecific diversification, along what could be called a good natural experiment. This lizard has evolved in a scenario that covers more than 1000 km from North to South, exposed to very diverse biogeographic and paleoclimatic historical conditions. It has arboreal tendencies, and it is oviparous. It is distributed in Chile from the Coquimbo Region in the north (Mediterranean shrublands landscapes, ca. 30° S) to the humid forested area of the Los Ríos Region (approx. 41° S), with some peripheral populations on the eastern slope of the Andes, in the Province of Neuquén, Argentina. Altitudinally, it extends from sea level on the Pacific coast to the Andean foothills. Although some populations can reach 1800 m.a.s.l., in most cases, it does not exceed 1000 m. This lizard has a remarkable ecological versatility, and it is abundant both in arboreal vegetation and scrubland, as well as in urbanized environments (Pincheira-Donoso and Núñez 2005). Adults show an evident sexual dichromatism. The male is of an extremely striking color, which makes it easily distinguishable, with yellow, green, and blue spots (Fig. 10.6). Two subspecies have been argued fundamentally for their patterns of dorsal coloration (Müller and Hellmich 1933): *Liolaemus t. tenuis*, from the Mediterranean environments of Santiago, approx. 33° S, and *L. t. punctatisimus* with type locality on the coast of the transition climatic zone in the Biobío Region (Lota, approx. 37° S). However, these lizards show a rather clinal variation, where the green tones increase toward the south, which does not ratify both subspecies from this point of view (Vidal et al. 2007). A geometric morphometrics study showed that populations from the humid range in the south differ slightly in its head shape from the rest of their populations (Vidal et al. 2005). Although, according to the above, *L. tenuis* shows some phenotypic variation, this variability is not distributed with a clear geographical structure. This is a morphologically conservative species considering its wide geographic range. Contrary to what its morphology suggests, *L. tenuis* is genetically a very variable species. This was already suggested by a study of isoenzymes which showed a tendency to group populations according to their latitudinal range (Vidal et al. 2004). The recently published phylogeography for this species shows suggestive arrangements of the important role played by geography and climatic changes of the Pleistocene in south-central Chile (Muñoz-Mendoza et al. 2017). This study covered the entire distribution of the species with a dense sampling (84 localities) and was based on mitochondrial and nuclear genes, plus five microsatellites. The geographical distribution of their lineages suggests

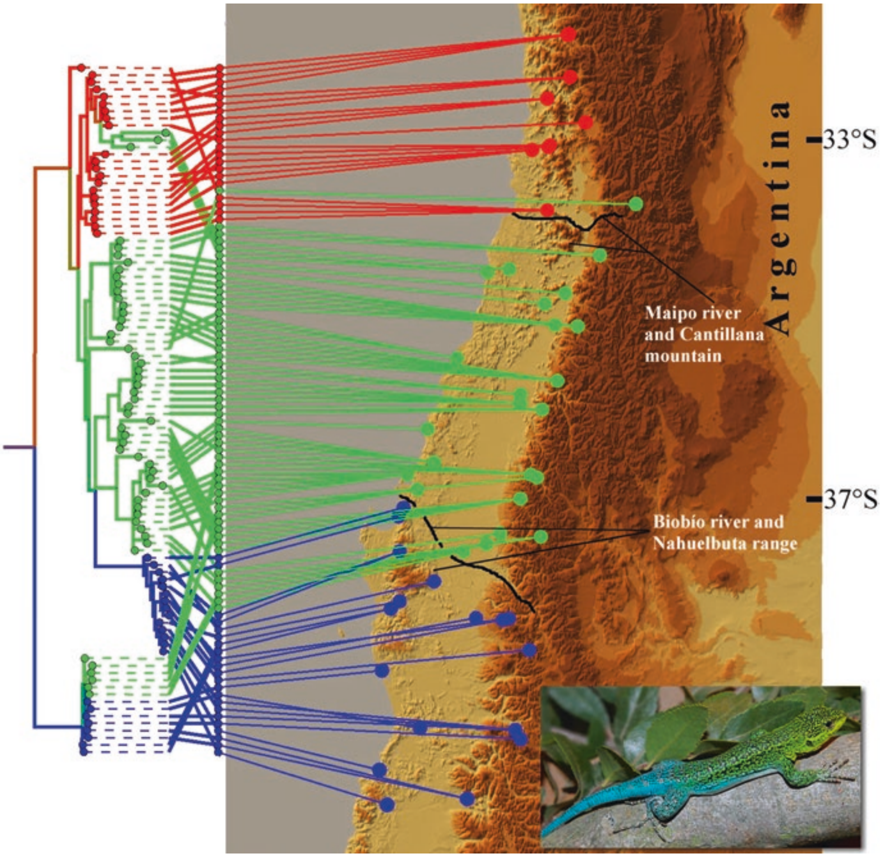

Fig. 10.6 Lineages distribution of *L. tenuis* and its association with the main river-mountains barriers in Central-southern Chile

important phylogeographic breaks associated with some Chilean rivers and mountains, among which the Maipo River (approx. 34° S) and the Biobío River (approx. 37 °–38° S) stand out (Fig. 10.6). Both fluvial systems have previously been hypothesized as probable barriers for other species. An additional interesting pattern in *L. tenuis* is its high number of lineages, several with deep divergences, and geographically structured, predominantly in the central-northern area of its distribution. The mitochondrial genetic diversity of the species would have an approximate age of 1.8 million years, when its two main lineages would have diverged. The first clade has a wide geographic distribution that covers almost the entire range of the species and whose diversity would have originated approximately 1.3 Ma. The second clade is typical of the wet zone, south of 37° S, and it is sympatric with the southern part of the previous clade (Fig. 10.6). This southern clade corresponds to a much more recent lineage (ca. 200,000 years), and its distribution coincides with an area where the ice sheet of the LGM acquired greater continuity (Rabassa et al. 2011).

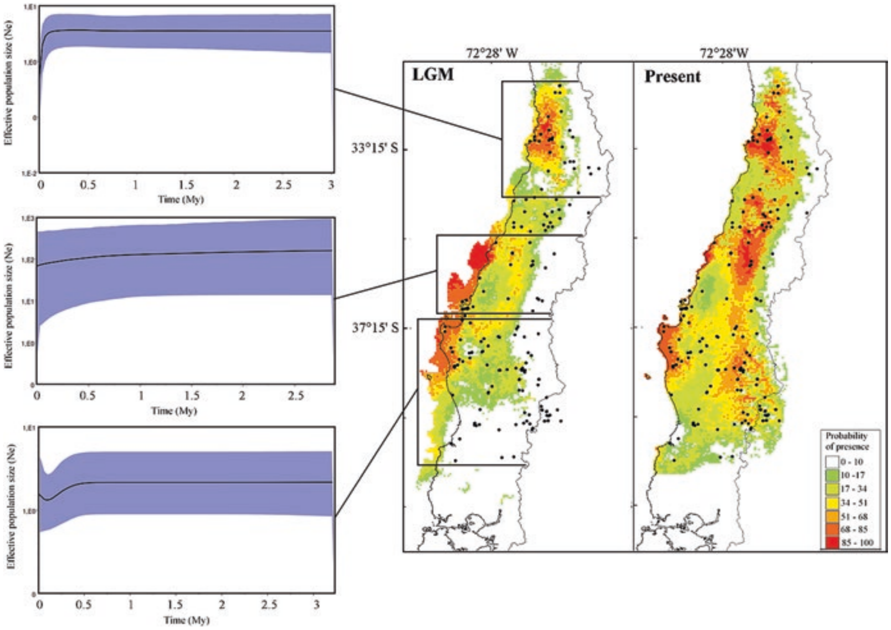

Fig. 10.7 Estimates of the historical variation of the effective population size (Ne) for the three main clades of the lizard *L. tenuis* (left) and ENM maps for the species (right) (adapted from Muñoz-Mendoza et al. 2017)

In contrast to the central-northern populations, there are interesting signs of recent recolonizations in the species austral range and, apparently, their historical demographic behavior has included considerable reductions in their effective population sizes, suggested by both analysis of Bayesian Skyline Plot and by past and present habitat suitability modeling (Fig. 10.7) (Muñoz-Mendoza et al. 2017). This is an interesting phylogeographic pattern that is consistent with the paleoclimatic history and geographic attributes of central-southern Chile, as narrated in a previous section of this chapter. The most stable areas for this species tend to be distributed at low altitudes, north of the Biobío River and near the Pacific coast (Fig. 10.7). According to the environmental history from south of Araucanía (approx. 38° S), where the two main lineages of *L. tenuis* are co-distributed, this species has experienced recent recolonizations from refugia, with range expansions, which resulted in a large secondary contact zone. The estimated patterns of historical gene flow are concordant with the above, where not only coastal populations would have functioned as a source in the south, but relict populations within the ice limit in the Andes would have recolonized from east to west. The geographical boundary concordant with the oldest divergence within *tenuis*, close to the Biobío River and to the northern edge of the Nahuelbuta mountain range, seems to have functioned as a complex of barriers in interplay with a climatic transition zone.

Apparently, this could be a good scenario to address not only phylogeographic questions but from a geogenomic and phylogeological point of view (Acosta et al. 2014; Baker et al. 2014; Fritz and Baker 2017). At this latitude, in addition to the Nahuelbuta range, part of the Coastal Range extends inland, approaching the Andes and narrowing the valley. Also, in this area there is a series of at least three deep fluvial canyons that cross the Intermediate Depression (e.g., Collipulli), which, in the past, during phases of rainiest times and melting (e.g., during meltwater pulses, after the LGM, from 15,000 to 8000 years ago; Fig. 10.3c; Fleming et al. 1998), could form a set of barriers. If a greater effect of the glaciations from this latitude to the south is added, the sum of all these factors could explain the phylogeographic discontinuity in this part of the *L. tenuis* distribution. For this area, reduced range of habitat and decreases in effective population sizes in Araucanía during LGM have also been detected in the lizard *L. lemniscatus* (Coronado et al. unpublished data). In addition, the distribution of intraspecific lineages coinciding with this latitude largely agrees with the delimitation of Chilean biogeographic units distinct to the south and north of such limit (e.g., Artigas 1975; Pisano 1954). This is indicative of environmental processes that have affected the intraspecific scale and would also have generated evolutionary effects at community level (species composition). For genetic and species diversity effects of environmental stability, there is published evidence for lizard assemblages from other parts of the world (Araújo et al. 2008; Werneck et al. 2012).

10.3.4 A Complex History in Forests and Islands

If we move to more humid and cold wooded environments of Chile, where lizard species decline in their richness, we find a very interesting history of refuges, vicariances, and dispersions. *Liolaemus pictus* is a species adapted to temperate forests dominated by *Nothofagus* and also inhabits *Araucaria araucana* formations. This lizard is distributed from sea level to 1600 m and in Chile it ranges from the Andes of the Maule Region (approx. 35° S in Alto Huemul Sanctuary; Ramírez-Álvarez and Troncoso-Palacios 2016), to the region of Los Lagos (approx. 43° S) (Vera-Escalona et al. 2010). In its southern distribution, this species inhabits both continental environments and the islands of the Chiloé archipelago. It is also present in the Province of Neuquén, Argentina, on the eastern slopes of the Andes, in forest environments that communicate with Chile through trans-Cordillera valleys. Approximately 50% of the area of its current distribution would have been covered by ice at the LGM. Both the geographical distribution and the moderate vagility of *L. pictus* suggest that it had to endure important evolutionary consequences due to the glaciations. This lizard shows an accentuated variation of coloration, which has motivated the description of six subspecies. Although one of them is already addressed in the literature as a distinct species (*L. septentrionalis*; Ramírez-Álvarez and Troncoso-Palacios 2016), given its evolutionary closeness and lack of a formal description, for purposes of phylogeographic analysis, it is treated in this chapter as part of *L. pictus*. The adaptations of these lizards that enable them to inhabit colder environments in comparison to other *Liolaemus* include its viviparous reproduction, and studies on its thermal ecology indicated it as a species with plasticity and low thermal requirements, even depending on which clade is involved (Artacho et al. 2017). Evidence suggests that populations of higher elevation environments show lower activity temperatures than those of low environments (Gutiérrez et al. 2010; Labra 2015), suggestive of adaptive variations according to the climate regimes to which different populations have been exposed. Little is known about their behavior and ways of communication. Labra (2015) indicates that, as it is true in general for *Liolaemus*, its displays are relatively simple in comparison to other groups of lizards. *Liolaemus pictus* is often observed in syntopy with *L. tenuis*, in relatively open wooded habitats, against which it tends to behave aggressively, imposing its larger size. Its isolation in several islands of the Chiloé archipelago seems to have generated interesting morphological and physiological differentiations (Vidal and Sabat 2010). According to comparisons using geometric morphometrics, this species shows significant differences in the cephalic shape (e.g., size of the eye orbits), which has been explained by allusions to adaptations to a differential use of resources between islands and the continent (Vidal et al. 2006). *Liolaemus pictus* is a relatively young species. An estimate based on the mitochondrial gene Cyt-b indicates that the age of the most recent common ancestor is 750,000 years (Vera-Escalona et al. 2012), which is notoriously lower than other *Liolaemus* species (see Olave et al. 2017). Another divergence age estimate based on the same gene suggests divergence between the populations of the Isla Grande de Chiloé and its neighboring islands in no more than 860,000 years (Vidal et al. 2012a, b). The woody landscapes in southern Chile generally appear to be composed of communities and taxa younger than the Mediterranean biota, based both on their vegetational composition and on assemblages of invertebrates (Markgraf and McGlone 2005; Segovia et al. 2013; Whitlock et al. 2001). This has been interpreted as a consequence of a fluctuating paleoclimatic history, which could also have influenced the origin and diversification of *L. pictus*.

The oldest divergence for the two main clades within *L. pictus* would have occurred during the second half of the Pleistocene, whose geographical limit, like *L. tenuis*, coincides with the north of the Araucanía at the latitude of Malleco, an area for which the probable role of a complex of old barriers was previously discussed in this chapter. The first of two main clades (North clade) extends from the north of the Araucanía at the Llaima Volcano (38° 41′ S) to the Maule Region, the northernmost limit of the species (approx. 35° S), in the *Nothofagus* forests that extend to the north progressively more discontinuously along the Andes. In this lineage are also included the populations of the Nahuelbuta coastal massif. Although, after the work of Vera-Escalona et al. (2012), all this northern lineage was suggested for *septentrionalis*, it is interesting the existence of considerable divergences within this clade, which perhaps should be reevaluated against the eventual existence of more than one taxon. At least three well-differentiated clades with allopatric distribution are distinguished in this northern group: one for Nahuelbuta, another for the Andean from the Llaima Volcano in the Malleco National Reserve, and a third for

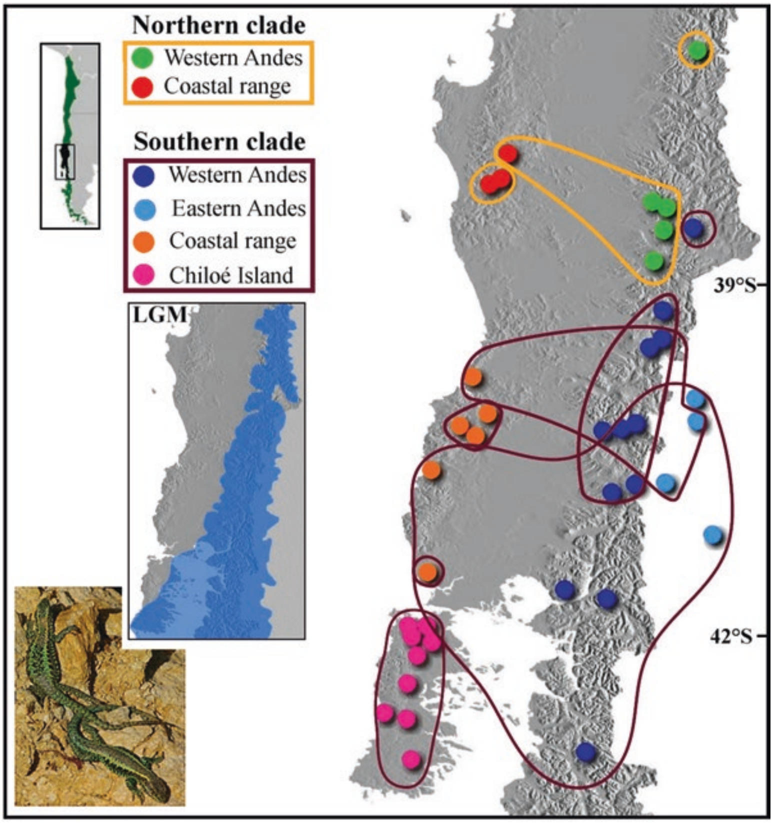

Fig. 10.8 Geographic distribution of the mitochondrial clades of the lizard *L. pictus*. The extension of the ice during the LGM is also shown

the valley of Las Trancas in Ñuble (Fig. 10.8). The notorious differentiation between these populations could well have been due to the cyclical range expansions of the forests whose distribution changed during the glaciations, expanding to the north during colder and wetter periods (Villagrán 2001); after their retreat to the south, during interglacial phases, left fragmented populations that would have promoted evolutionary divergence. Being part of one of the distributional extremes of the species, this pattern could be explained by the "central marginal hypothesis," which proposes that peripheral populations tend to be associated with greater and more frequent events of demographic instability, smaller effective population sizes, and with greater genetic differentiation (Eckert et al. 2008). The second main clade of *pictus* (austral lineage) covers a much more extensive territory (Fig. 10.8), from the north of Araucanía (approx. 39° S) to insular and mainland Chiloé in the south (ca. 44° S). Three interesting aspects of the history of *L. pictus* can be read in the topology of this great southern lineage, which is evidenced by estimates of gene flow, structuring patterns, historical population sizes, and inferred historical geographic distribution. The notorious absence of reciprocal monophyly between populations from the Andes and from the Coastal Range, where even populations in the Argentine side are closely related to the coastal populations of Chile, is suggestive of a complex historical connection between the populations of both mountain ranges. Important magnitudes of bidirectional historic East-West gene flow, coupled with an increase in habitat suitability in the valleys of the Intermediate Depression during the LGM, suggest that these populations were able to recurrently connect. A dynamics of descent into the valleys during the glaciations and subsequent recolonization of mountain ranges during interglacial periods has been hypothesized for trees in this area, such as for *Austrocedrus chilensis* (Souto et al. 2015; Pastorino and Gallo 2002) and *Araucaria araucana* (Ruiz et al. 2007), both species that are part of the *pictus* habitat. Greater historical connectivity compared to the demographic behavior of the northern populations, and compatible with range expansions in the south of the *L. pictus* distribution is suggested by a latitudinal gradient of differentiation according to a genetic landscape analysis, with less structuring toward the south (Fig. 10.9). This is consistent with estimates of a greater historical reduction in effective population size during the LGM in the southern lineage (based on Bayesian Skyline Plots). A second interesting aspect is that apparently *L. pictus* would have persisted in numerous intraglacial refugia (cryptorefugia and/or microrefugia), from which it would have expanded its range during the interglacial phases. As in *L. tenuis*, although in *pictus* it would have been much more evident and extensive, such refugia would have worked as sources that contributed genetic variability to lower areas, and even to those of the Coastal Range. As previously indicated, the evidence of glacial refugia has been indicated for different taxonomic groups, such as for the rodent *Abrothrix manni* (Valdez and D'Elía 2018), trees (Allnut et al. 1999; Arana et al. 2010; Bekessy et al. 2002; Pastorino and Gallo 2002; Marchelli and Gallo 2006), freshwater fishes (Cussac et al. 2004), amphibians (Nuñez et al. 2011), and crustaceans (Xu et al. 2009). The recolonization of *L. pictus* from different continental refugia was also suggested by Vidal et al. (2012a, b) in a beautiful phylogeographic reconstruction for the austral range of the species. A third emergent attribute in the spatial arrangement of lineages of *L. pictus* is the lack of molecular evidence to support the existence of most of their subspecies previously based on morphology, although with two clear exceptions associated with their distributional extremes. One of them was already highlighted, which is the case of northern *septentrionalis*, and the other is the case of southern *chiloensis* subspecies, on the Isla Grande de Chiloé (approx. 42° S–44° S). Although it is not a complete reciprocal monophyly, most of the genetic diversity of the Isla Grande de Chiloé is exclusive for this island and forms a clade of considerable divergence. Although during each glaciation the sea descended, being able to connect islands with the continent at that latitude (Pirazzoli 1991), apparently the phylogeographic signals (and not only for *L. pictus*), do not clearly shows that. Even for larger species such as the Andean southern deer *Pudu pudu*, a large molecular divergence was detected for this species between the population of the island and the continent (Fuentes-Hurtado et al. 2011).

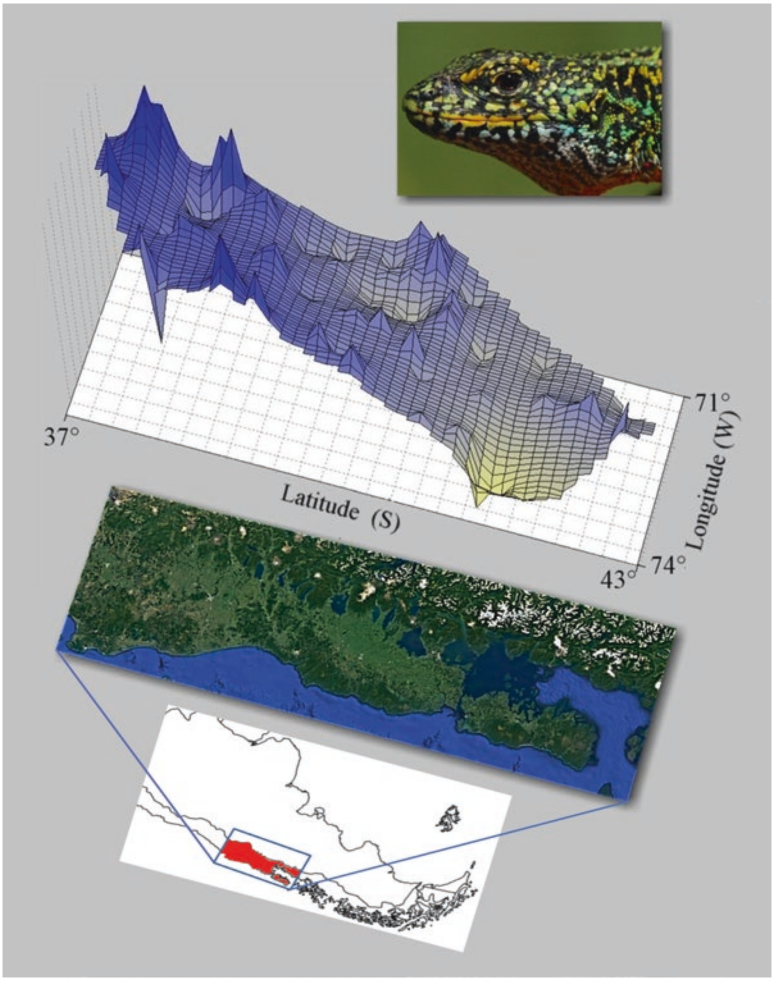

Fig. 10.9 Genetic landscape shape interpolation analysis for the distribution of *Liolaemus pictus* based on mtDNA. Blue and high areas in the graph correspond to higher levels of genetic structuring. Low and yellowish areas correspond to low genetic structure

Given that the sea descended repeatedly, establishing island-continent bridges, a vertebrate of that body size should show fewer structuring signals. Vidal et al. (2012a, b) also detected strong structuring for *L. pictus* between the Chiloé Island and the mainland, dating it as a divergence predating the LGM. Although such an evolutionary divorce is indicated as previous to the last glaciation (ca. 860,000), the marked evolutionary differentiation of these populations was explained by a probable recent configuration of the shallow continental shelf. If so, this scenario would not have provided the conditions to form land bridges for a sufficient time to generate island-continent exchanges in *L. pictus*. However, in relation to the age of this species, the Chiloé-continent disconnections encompass most of the evolutionary history of this lizard. A complementary explanation for this great structuring is that either no continuous terrestrial connection was established with the continent, or if it happened, the emerged shelf did not come to form a continuous ecosystem compatible with species highly dependent of a dense forest ecosystem. Evidence based on microsatellites and mtDNA in the small felid *Leopardus guigna* suggests that this cat has had greater connectivity between the Island of Chiloé and the continent (Napolitano et al. 2014). This is a species that, although it is an inhabitant of the forest, is a more generalist in habitat use than *L. pictus*, being able to be detected in more open environments, such as scrub and savanna (Iriarte et al. 2013). The dynamics of colonization of the other small islands of the Chiloé archipelago by *L. pictus* has been somewhat different, where there would have been greater levels of connectivity, both with the mainland and with the Isla Grande de Chiloé. Vidal et al. (2012a, b) explained such minor structuring, alluding that terrestrial connections were more likely, where the genetic composition of such islands suggests a complex history of young colonization routes (even after the LGM), both from the mainland and from Isla Grande de Chiloé. In summary, the phylogeography of *L. pictus* is a good example in which the diversification within a lizard species has gathered different patterns and processes depending on its geographic range. In the north of its distribution, it would have been affected by the distributional dynamics of the forests (expansion-contraction), due to past climatic changes. In its central range, an Andean-Coastal exchange dynamic is highlighted, including intraglacial refugia, and in the insular southern range populations, the changes in sea level, the presence of extensive glaciers, and their thaws would have formed a complex history of barriers and land bridges.

10.3.5 Comparative Phylogeography: Shared Histories in Co-distributed Lizards

Comparative phylogeography (CP) aims to investigate the eventual spatial and temporal agreement of divergence processes and demographic histories of two or more co-distributed species (Gutiérrez-García and Vázquez-Domínguez 2011). In this sense, CP has much to contribute to historical biogeography by gathering evidence of processes that could explain the concordances in spatial distribution of genetic diversity at the community level (Arbogast and Kenagy 2001; Zink 2002). For example, it can identify suites of species that have had a common vicariant history (Moritz and Faith 1998). CP could also be complemented with comparative studies of the phylogenies of community structure, establishing in this way a link between the community ecology and biogeography (Vamosi et al. 2009). Another contribution of CP is that, through its multispecies approaches in common scenarios, it takes advantage of natural experiments, where replicates of species (independent evolutionary units that provide genetic response variables) are useful to infer generalizable processes that can be tested statistically (Bermingham and Moritz 1998). Since its inception, when CP simply consisted of visually contrasting the topologies of different co-distributed species, it has progressed to include sophisticated methods that statistically evaluate hypotheses about common evolutionary histories. The first statistical evaluation estimated the significance of congruent areas-topologies and the construction of supertrees to delimit geographical areas with common evolutionary histories for the species they harbor (Lapointe and Rissler 2005). With the emergence of statistical phylogeography (Knowles and Maddison 2002; Knowles 2004), which considered the use of summary statistics in the frame of coalescent stochasticity, the evaluation of hypotheses of simultaneous and co-distributed vicariances for different species was strengthened (Hickerson et al. 2006). A good example of this approach is the study by Carnaval et al. (2009), which provided evidence for codivergences between amphibian species of the Atlantic coast of Brazil. The incorporation of nongenetic evidence, such as ecological niche models (ENM), has allowed us to evaluate if the historical distribution of populations of different co-distributed species is correlated. If it is a positive result, and if it is consistent with the distribution of lineages of several species, we have evidence that environmental history has influenced co-diversification processes between species (Carstens and Richards 2007; Knowles et al. 2007). CP studies in Chile are still very scarce, and it represents a potentially fertile ground to understand the processes that have affected lizard assemblages as a whole (or for lizards and other kinds of organisms). Although an interesting number of individual studies for plants and animals from Chile have already been published (several of them with wide distributions and co-distributed), the comparative approaches do not exceed four cases.

According to a compilation of phylogeographies for terrestrial vertebrates and plants, which qualitatively integrates publications of co-distributed species (Sérsic et al. 2011), some congruent patterns suggest that quaternary and pre-quaternary geological events would have promoted the concerted diversification of some taxa in southern South America. Victoriano et al. (2008) found evidence that three species of *Liolaemus* (*L. tenuis, L. lemniscatus,* and *L. pictus*) show significant topological agreement for some of their clades. A supertree based on the integration of the topologies of these three lizard species also showed concordance with the main Chilean bioclimatic zones (mesomorphic, transition, and hydromorphic). These three species showed a significant correlation between the patristic distances of the supertree and the bioclimatic similarity between such areas (Fig. 10.10). As such, we can think that each Chilean bioclimatic zone harbors singular evolutionary histories of their biota, which is interesting both from a biogeographical point of view as well as regarding proposals for conservation areas. This study also suggests that in the Mediterranean area in central Chile, the pair *L. tenuis-L. lemniscatus* could have co-diversified in response to shared vicariant events, which would have been predominant over the effects of glaciations. A study previously commented on in this chapter indicates that important barriers for the divergence of the main clades of *L. tenuis* are due to rivers and mountains (Muñoz-Mendoza et al. 2017).

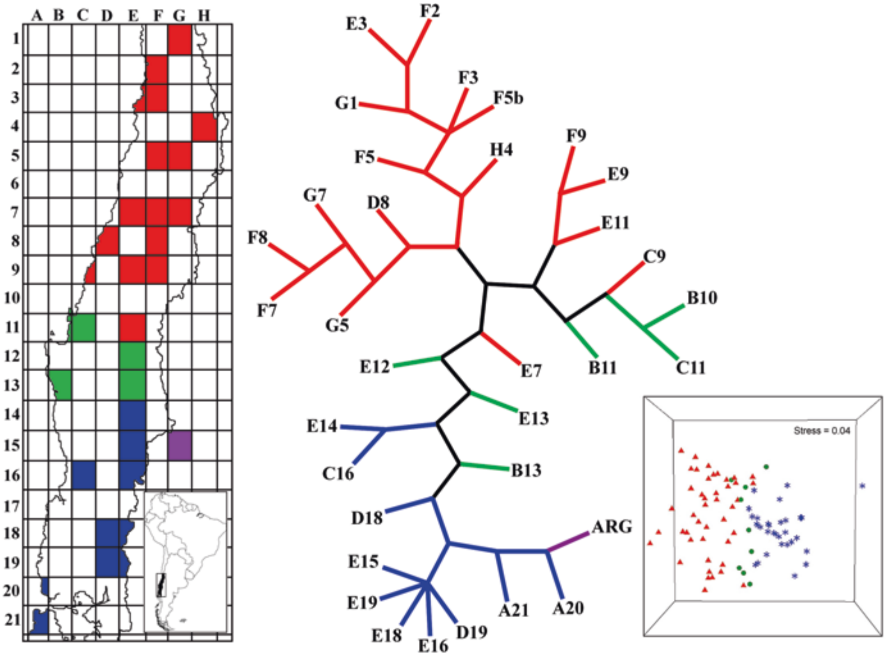

Fig. 10.10 Supertree of areas based on mitochondrial sequences of the species *L. tenuis, L. lemniscatus,* and *L. pictus*. The acronyms of letters and numbers correspond to the quadrants shown on the map. The colors correspond to general bioclimatic zones of Chile. Red, mesomorphic; green, transitional; blue, hydromorphic or wet zone; violet, Argentinean populations. Below to the left is a multidimensional scaling for localities of the three Chilean zones, based on bioclimatic similarity

The processes that would have affected in a similar and contemporary way these two co-distributed *Liolaemus* could generate not only simultaneous vicariance but also demographic changes in parallel, for example, trends of past changes in their effective population sizes. When associating the values of effective population size of same date estimated by BSP for *tenuis* and *lemniscatus*, a significant positive correlation is observed. This is indicative that past environmental factors generated at the same time result in changes of abundance in both species in similar ways. Further south in the hydromorphic zone, for the species pair *L. tenuis-L pictus*, the glacial cycles would have been those that predominantly structured their shared phylogeographic history, where heterospecific populations could share a history of marked environmental instability promoting concerted diversification. This is corroborated by observing changes in the habitat distribution of both species during the LGM, suggested by niche modeling (Muñoz-Mendoza et al. 2017; Vera-Escalona et al. 2012). For this geographic range there is also phylogeographic evidence for other two species, *L. pictus* and *L. cyanogaster*, with concordant evolutionary responses that occurred during the Middle Pleistocene (Vidal et al. 2012a, b). Within this same area, including the Chiloé archipelago, the complex interaction between the quaternary glacial cycles with geography would have generated concordant phylogeographic patterns between the lizard *L. pictus* and the amphibian *Batrachyla leptopus*. It is really interesting that taxa of contrasting biologies could suffer similar evolutionary consequences (Vidal et al. 2016). Among the common processes for this lizard-anuran pair, there is the apparently simultaneous divergence of populations of Isla Grande de Chiloé with respect to the continent, a complex colonization dynamic of the small islands, and the occurrence of refugia both on the Pacific coast and east of the Andes. CP studies in Chile suggest that this scenario could have generated common evolutionary histories, not only for lizard species but for other components of the community. As previously mentioned, there are phylogeographic studies of several taxa that share a large part of their distribution, including plants, terrestrial vertebrates, and invertebrates, which are available to test hypotheses of concerted evolution at community level. Among the interesting geographical scenarios of the west of the Andes that could be evaluated regarding its diversifying role is the aforementioned phylogeographic break south of the Biobío River in the northern limit of Araucanía. However, such spatially concordant differentiation patterns could respond to very different times throughout the complex geological and climatic history of a sum of both new and old barriers. It also seems interesting the evaluation of the probable role of the numerous rivers arranged latitudinally in Chile, which in interaction with the relief seem to have been relevant in the case of lizards (Muñoz-Mendoza et al. 2017; Torres-Pérez et al. 2009). Finally, and far from exhausting the options for hypotheses, the questions about simultaneous multispecies processes of population retraction and recolonization in the glaciated range are pending. All these questions should be addressed, beyond verifying topological congruences, using coalescent approximations (ABC), which would allow us to estimate whether spatial patterns of diversity have been generated at similar times or have obeyed differentiated events in time. It is also necessary to incorporate multilocus evaluations, ideally through NGS methods, in order to base conclusions on a broad genomic coverage.

10.4 Phylogeography and Lizard Conservation

Biodiversity conservation initiatives should pay attention to all levels of organization, including genetic diversity and intraspecific lineages, so as to ensure the persistence of viable populations and to ensure their evolutionary and adaptive potential (Rodrigues and Gaston 2002). Until now, reality is far from this, and the greatest effort has been made to maximize species richness and endemism (Purvis and Hector 2000; Ricklefs and Schluter 1993). From this point of view, phylogeography contributes mainly in two aspects: first, detecting intraspecific diversity and its geographical distribution, which is fundamental for prioritizing territorial units of conservation, and second, understanding the history and factors that have generated intraspecific diversity. The latter is fundamental because understanding the past can be of great help to infer the future behavior of populations in the face of ongoing environmental changes. For example, one of the key aspects that could be affecting the populations of lizards is the change in land use (Chap. 14). The performance of some *Liolaemus* depends on the type of vegetation (Fuentes and Jaksić 1980; Medel et al. 1988), and the anthropogenic changes of vegetational structure could be significantly altering their behavior, abundance, and distribution (Mora and Labra 2017; Rubio and Simonetti 2011; Uribe and Estades 2014; Chap. 5). An example about this is the revision of the historical distribution of *L. pictus*, whose geographical range would have been considerably reduced (Vera-Escalona et al. 2010), as a probable consequence of the elimination and fragmentation of the native forest (Echeverria et al. 2006; Armesto et al. 2010). In this case, we do not know which intraspecific lineages became extinct during this process.

One of the phylogeographic paradigms states that areas of greater genetic diversity would be associated with scenarios with higher historical environmental stability (Carnaval et al. 2009), which apparently also extends to the richness of species (Werneck et al. 2012). The foregoing seems to be the case of the Chilean Mediterranean area, where, unlike the southern zone most affected by the glacial cycles, its populations would have experienced smaller distributional changes and fewer reductions in their abundances. If we consider an estimate of genetic conservation value (GCV) based both on genetic diversity and haplotype singularity (Fig. 10.11), those areas with the greatest GCV should be prioritized. According to estimates of the geographical distribution of this index in three *Liolaemus*, a large part of this diversity is concentrated in the unprotected Mediterranean zone. On the other hand, a trend toward lower values of this indicator has been observed in areas where glaciations have shown signs of impoverishment and genetic homogenization. A good example of this pattern is the geographic distribution of GCV in *L. pictus* (Fig. 10.11).

Previous detection of cryptic diversity in *Liolaemus* (e.g., Olave et al. 2017; Torres-Pérez et al. 2009), and the recent description of new species for Chile (Esquerré et al. 2013; Troncoso-Palacios et al. 2015, 2016), suggests that a large part of the diversity of lizards is not yet known for southern South America. In this sense, phylogeography is contributing much to the complex process of delimiting species. An example of phylogeographic evidence with consequences for the conservation of a lizard in Chile is the confirmation that the northern populations of *L. pictus* (currently *L. septentrionalis*) should be considered as a different species with a need to conserve. Something similar is the case of the *L. pictus* lineage of Isla Grande de Chiloé, although in this case it is a subspecies. For Chilean herpetozoans, the spatial delimitation of evolutionary conservation units (ESUs; Crandall et al. 2000; Moritz 1994) has been explicitly evaluated only for one species of snake (Sallaberry-Pincheira et al. 2011), while for lizards this aspect has only been collaterally commented in phylogeographic studies. For example, an interesting number of lineages have been detected in the northern central range of distribution of *L. tenuis* and *L. lemniscatus*, most of them in the Mediterranean area with the largest human population and the largest alteration of the landscape. This is a paradox in conservation because the coverage of the National System of Protected Areas (SNASPE) in Chile, which tends to increase toward the south of the country

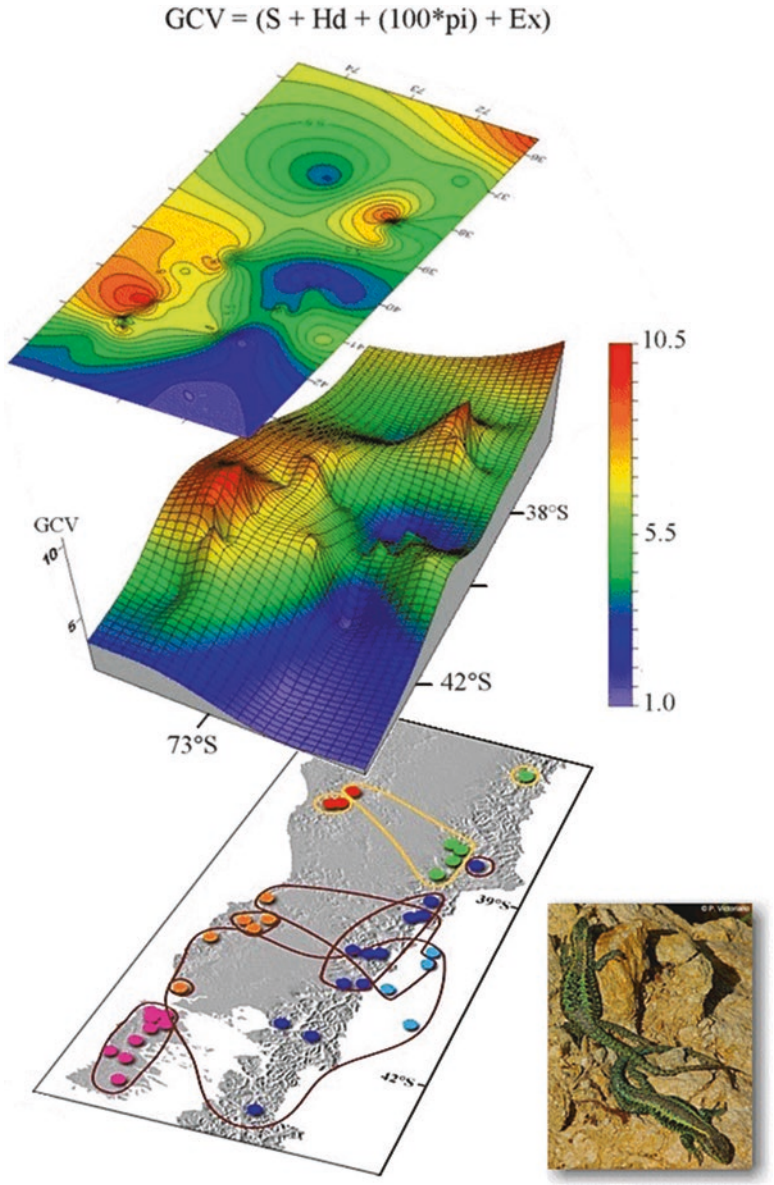

Fig. 10.11 Geographic distribution of genetic conservation values (GCV) for the lizard *L. pictus*. The geographical distribution of lineages is also shown. *S* haplotype richness, *Hd* haplotype diversity, *pi* nucleotide diversity, and *Ex* number of private haplotypes

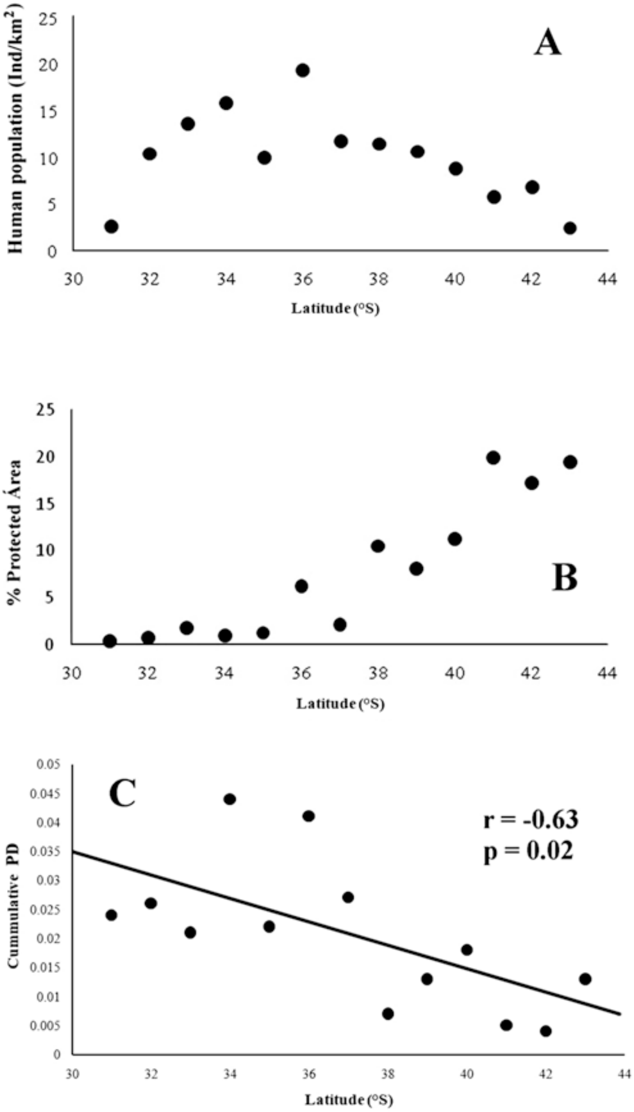

Fig. 10.12 Latitudinal trends of (**a**) human population density and (**b**) of protected areas surface in central-southern Chile. In the bottom (**c**), the correlation of the accumulated phylogenetic diversity for the lizards *L. tenuis*, *L. pictus,* and *L. lemniscatus* with latitude is shown

(Fig. 10.12b), would not be protecting much of the intraspecific diversity of central Chile.

Due to its high richness and endemism, as well as the high and progressive degree of anthropic intervention, central-southern Chile is considered as one of the 25 hot spots of terrestrial biodiversity (Myers et al. 2000; Smith-Ramírez 2004). One criterion for prioritizing conservation areas is the evolutionary or phylogenetic diversity index (PD; Faith 1992). According to this criterion, those areas that include a higher genealogical diversity (probably generated over a longer evolutionary time) should be considered as more valuable. Taking this into an intraspecific context, when looking at the geographic tendencies of DF in three species of *Liolaemus* from central-southern Chile, a negative correlation of this index was observed with latitude (Fig. 10.12c) (Victoriano et al. 2012). In this regard, the quantification of the intraspecific phylogenetic diversity of lizards that would be protected within the SNASPE and the estimation of the percentage that is exposed to be eliminated are still pending. This kind of estimate was made for the amphibian *Telmatobius marmoratus* in northern Chile, where it was evident that a large part of its evolutionary diversity is unprotected (Victoriano et al. 2015). On the other hand, according to phylogeographic evidence, species of *Liolaemus* have been sensitive to the climatic changes of the past, which suggests that they are exposed to important negative consequences as a result of the ongoing anthropogenic climate change. The substantial difference between the natural processes of the past and those induced by humans is that the latter are occurring at a speed incompatible with the evolutionary response capacity of the species. A considerable number of lizard populations in the world have already become extinct due to global warming and, according to complex models, for the near future many of them have a high probability of disappearing, including Chilean *Liolaemus* populations (Sinervo et al. 2010). A useful initiative in this sense would be the overlap of phylogeographies with extinction probability maps, which could provide us with an idea of how much and what intraspecific evolutionary diversity could go extinct in the coming decades. A comparable approach is proposed by Brown et al. (2016), which aims to predict the genetic consequences of climate change, integrating coalescent approaches, spatiotemporal variations of demography, and estimates of landscape changes. Although classical molecular methods can still contribute much to the conservation of lizards, with the increasingly frequent use of genomics (NGS), more sophisticated options open up, for example, the use of the transcriptome, SNPs, and evaluation of loci with adaptive value. However, the direct application of genomics in the field of conservation is still in early development (McMahon et al. 2014).

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Chapter 11
General Ecology of Patagonian Lizards

Juan Carlos Acosta, Rodrigo Gómez Alés, Graciela Blanco, Paula C. Escudero, and Luciano J. Avila

Abstract Reptiles have physiological, morphological, and behavioral adaptations that allow them to survive in desert environments, at high altitudes and in cold climates, such as the Patagonia region in southern Argentina. Knowledge of the ecology of Patagonian lizards is limited and fragmentary. The objective of this chapter is to present a synthesis of the current state of knowledge of the ecology of Patagonian lizards with regard to the use of (1) spatial resources (home range, use of microhabitats), (2) temporal resources (daily and seasonal patterns of activity), and (3) trophic resources (diet and nutrition strategies). We also discuss inter- and intra-species interactions, including predation, seed dispersal, parasitism, behavior, and resource partitioning.

Keywords Diet · Habitat · Use time · Behavior · Predation · Parasitism · Seed dispersal · Competition · Resource partitioning · Teiidae · Liolaemidae · Phyllodactylidae · Leiosauridae

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J. C. Acosta · G. Blanco
Gabinete Diversidad y Biología de Vertebrados del Árido (DIBIOVA), Departamento de Biología, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de San Juan, San Juan, Argentina

Centro de Investigaciones de la Geósfera y la Biósfera (CIGEOBIO-CONICET) Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de San Juan, San Juan, Argentina

R. Gómez Alés (✉)
Gabinete Diversidad y Biología de Vertebrados del Árido (DIBIOVA), Departamento de Biología, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de San Juan, San Juan, Argentina

Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Buenos Aires, Argentina

P. C. Escudero · L. J. Avila
Instituto Patagónico para el Estudio de los Ecosistemas Continentales – Consejo Nacional de Investigaciones Científicas y Técnicas (IPEEC-CONICET), Puerto Madryn, Chubut, Argentina

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11.1 Introduction

The structure of communities is modeled on both historical and ecological factors. Ecological factors mainly include interactions among sympatric species and their relationships with the local environment, which in some cases can result from the segregation of the basic resources utilized by the species (food, microhabitat, and activity time; Pianka 1973; Schoener 1974; Mesquita et al. 2015; Winck et al. 2016). In addition, differences between how sympatric species utilize available resources may be influenced by the community itself (ecological factors) and/or can be a reflection of an historic divergence (historical factors; Vitt et al. 1999; Vitt and Pianka 2005; Pinho Werneck et al. 2009). Availability and resources acquisition may vary in time and space, in accordance with behavior of consumers, temporal differences in activity, and use of microhabitats (Winemiller and Pianka 1990). The dimensions that make up the ecological niches of lizards have evolved in tune with changes in their life histories and the patterns have been repeated. For example, lizards from the Australian desert resolve problems in the same way that African and American lizards do, even when they are not phylogenetically related (Pianka et al. 2017).

Although there is consensus about the need and importance of understanding these aspects of the herpetological communities in Argentina and Chile, and particularly in Patagonia, this information is scarce. There are only a few studies on some species with data that is frequently sparse. The objective of this chapter is to compile this information and integrate it in line with the aforementioned central concepts, in other words to present the data currently available on the use of spatial (home range, microhabitats), temporal (daily and seasonal patterns of activity), trophic (diet and nutrition strategies), and inter- and intra-species interactions (predation, parasitism, seed dispersal) and behavior.

11.2 Behavior and Activity

11.2.1 Behavior

The ecology of behavior is an enormous field of study that includes movements, social interactions, foraging, communication, and escape from predators, among others (Vitt and Caldwell 2013; Cooper and Blumstein 2015). Behavioral decisions that individuals make ultimately influence their aptitude, as they determine if an individual will be able to compete within its species' social system, avoid predators, or successfully find food (Vitt and Caldwell 2013). Within this field, communication is essential for understanding many other aspects, such as territorial defense, mate choice, conflict resolution, foraging, or antipredatory behavior (Font et al. 2010). In general, animals communicate using signals that can be visual, auditory, chemical, or tactile. In lizards, the chemical and visuals signals are the most studied;

however, there are some studies that focus on auditory signals (Pough et al. 2001; Labra 2008). Chemical signals (pheromones), dependent on the vomeronasal organ (Labra et al. 2005; Labra 2008; Mason and Parker 2010), play a fundamental role in many aspects of reptile biology, sexual recognition (Cooper 1994; Labra and Niemeyer 1999), territory marking (Halloy and Robles 2002; Fox and Shipman 2003), avoidance of agonistic encounters (Cooper and Vitt 1987; Halloy and Halloy 1997; Labra 2006), aiding in the location of shelter, detection of predators, selection of microhabitat, foraging, communication, and recognition of conspecifics (Labra et al. 2001b; Font et al. 2010; Vitt and Caldwell 2013). Different organs, femoral, precloacal, or urodaeal glands, can produce pheromones (Cooper and Trauth 1992; Cooper 1994; Sánchez-Martínez et al. 2007; Labra 2008). Less specific sources can also be involved such as the exudates of the body surface and feces (Mason and Gutzke 1990; López et al. 1998; Bull et al. 2000; Aragón et al. 2006; Labra 2008).

A Patagonian lizard as *Liolaemus lemniscatus,* for example, like in other *Liolaemus* species, displays a strong response to odors coming from individuals of the same species, that is, its exploratory behavior increases through tongue and head movements (Labra 2011). This could indicate that odors from conspecifics are relevant social signals and that chemical stimulants are involved in the recognition of species, a fact that could aid in maintaining the integrity of species and their reproductive isolation (Labra et al. 2001a; Johansson and Jones 2007; Smadja and Butlin 2009; Labra 2011). Chemical signals and their recognition could play an important role in the diversification of *Liolaemus*, as well as in maintaining its high diversity (Labra 2008). In the different environments of Patagonia, lizard assemblages occur with numerous species of *Liolaemus* living in syntopic conditions and with similar ecological and morphological characteristics, so the recognition of specific chemical signals would have a predominant role in reproductive isolation (Labra 2008). This has been documented in *Liolaemus bellii*, *L. jamesi,* and *L. lemniscatus*, species that differentiate between secretions of sympatric and allopathic conspecifics, suggesting that in sympatric conditions the possibility for hybridization between these *Liolaemus* species is low (Labra et al. 2001b; Labra 2008).

On the other hand, pheromone bioassays for *Liolaemus tenuis* (Fig. 11.1a) demonstrate that their fecal matter contains pheromones utilized for self-recognition, a fact that can be seen in individuals that present a lower number of tongue-flicks on rocks containing their own fecal matter, as opposed to rocks containing the fecal matter of other lizards or the control group. Likewise, *L. tenuis* males do not discriminate between their own precloacal secretions and those of other males, so the authors propose that secretions convey information to males of a “male presence” (Labra et al. 2002). Possibly, males make a latter finer recognition through feces. Alternatively, precloacal secretions may have evolved to convey information mainly detectable or relevant for females or that they convey important information mainly during the breeding season.

Some behaviors may be modeled by each sex within a species, as has been observed in *Liolaemus nitidus* (Fig. 11.1b). This is the case of responses observed in the presence of odors from a conspecific, which trigger greater chemical exploration in males as evidenced by shorter latency with the first hit of the tongue

Fig. 11.1 (**a**) *Liolaemus tenuis*, male (front) and female (back). (**b**) *L. nitidus* with broken tail (Chile). (**c**) *L. cuyumhue* sand-diving. Black arrows mark dorsum and tail. (**d**) *L. chiliensis*. (**e**) *L. curicensis* (Chile)

(Troncoso-Palacios and Labra 2012). This difference in reaction may be influenced by territoriality, as males experience greater selective pressure to recognize and react with individuals of the same sex (Troncoso-Palacios and Labra 2012). In contrast, in the presence of unknown odors or those of predators like snakes, *L. nitidus* responds by shaking its tail for a prolonged period of time or with "slow-motion" actions; both of these strategies help to ward off an attack on its tail by predators, either by losing the tail through autotomy or by reducing its detectability, respectively (Bateman and Fleming 2009; Troncoso-Palacios and Labra 2012). On the other hand, it has been observed that *Liolaemus* does have the ability to detect chemical secretions of snakes, but its responses are dependent on the predation pressure experienced by the species in their natural habitat (Labra 2008). *Liolaemus lemniscatus*, sympatric with the snake *Philodryas chamissonis*, reduces chemical exploration when exposed to snake secretions and shows a high frequency of antipredatory behaviors, which would reduce its detectability by a predator; on the contrary, *L. fitzgeraldi*, allopatric to *P. chamissonis*, does not show any sign of recognition of and behavior to secretions of the snake (Labra and Niemeyer 2004).

Regarding visual communication, two types of signals have been described in lizards: patterns of coloration and stereotyped movements. The first is generally linked to nuptial coloration or sexual selection, as in many *Liolaemus*, which reflects their reproductive state (e.g., *L. tenuis*; Vidal et al. 2007; Fig. 11.1a), or they may reflect dominance between males, as in *Liolaemus sarmientoi* where males with red coloration are more aggressive during agonistic encounters than those with yellow coloration (Font et al. 2010; Fernández et al. 2018). However, in another species *Liolaemus xanthoviridis*, individuals of both sexes are polymorphic in dorsal coloration (Escudero 2016) and ventral melanism (Escudero et al. 2016), but no evidence was found that this polymorphism represents different reproductive strategies linked to visual signals. Many lizards have vision in the near UV (e.g., Macedonia et al. 2000; Fleishman and Persons 2001; Font and Molina-Borja 2004; Molina-Borja et al. 2006; Whiting et al. 2006), that is, they are capable of perceiving ultraviolet radiation which improves the visibility of their coloration patterns, patterns which are only visible for receivers who have a visual system sensitive to that part of the spectrum (e.g., Harosi 1985; Burkhardt 1989; Yokoyama and Shi 2000; Hunt et al. 2001). The ability to see in the UV is a potentially important route for both intraspecific and interspecific communication and subject to sexual selection. The presence of a photopigment sensitive to UV has been confirmed in 13 species of iguanids, five geckonids, and four chameleons (Fleishman et al. 1993, 1997; Loew 1994; Ellingson et al. 1995; Loew et al. 1996; Bowmaker et al. 2005). In males of three species of *Liolaemus* lizards, *L. grosseorum*, *L. darwinii,* and *L. ruibali*, it has been detected the presence of coloration in the UV range in blue scales located in different parts of the body (Salica and Halloy 2010). However, there is no data regarding the ability of these lizards to perceive this type of coloration. In birds and reptiles, it has been recorded that some species are dichromatic in the visible and ultraviolet spectrum (e.g., Mays et al. 2004), while in others the dichromatism is only found in the ultraviolet region (e.g., Hunt et al. 1998; Thorpe and Richard 2001; Molina-Borja et al. 2006; Pérez de Lanuza and Font 2007). In *L. xanthoviridis,* males and females with similar coloration (e.g., “yellow”) could be dimorphic in the UV spectrum (Escudero 2016). Several studies have shown that UV colorations are important in intrasexual competition and in the choice of partners in birds, fish, and invertebrates (e.g., Siitari et al. 2002; Losey 2003), but their possible communicative function in reptiles remains relatively unexplored.

On the other hand, there are stereotyped movements. These are very important components of animal communication since deployments usually have a unique “signature” that allows conspecifics to identify each other, allowing individuals to focus on new rivals and not waste energy on known enemies (Husak and Fox 2003). The most common are the headbob display, the forelimb wave, and the tail movements (Font et al. 2010; Halloy et al. 2013). These movements, taken together or separately, are specific to each species and provide information about territoriality, mating, and antipredatory alerts, among other aspects (Carpenter 1978; Martins et al. 2004). They also provide information about the identity of the species, sex, reproductive state, and even individual identity (Halloy et al. 2013). Headbobs are easily distinguished as a series of stereotyped movements of the head up and down, sometimes accompanied by the trunk or by specific body positions such as an extension of the chin or raising of the tail (Martins et al. 2004). Headbobs have been observed in various Patagonian lizards, including *Phymaturus calcogaster* and *P. zapalensis* (Halloy et al. 2013), and in several *Liolaemus* species, including *L. elongatus*, *L. pictus*, *L. cuyanus*, *L. loboi*, *L. lemniscatus*, *L. darwinii*, *L. kingii*, *L. lineomaculatus*, *L. petrophilus*, and *L. xanthoviridis*, among others (Martins et al. 2004; Labra et al. 2007a; Halloy et al. 2013; Escudero 2016). For these lizards, a relatively simple headbob has been described, which may be accompanied by additional visual displays such as forelimb wave, tail movements, and tongue licking, in order to enrich possible messages to conspecifics (Martins et al. 2004; Labra et al. 2007a; Labra 2011; Halloy et al. 2013). Forelimb waving consists of a circular movement of one frontal extremity (though sometimes both frontal extremities are involved) and is generally associated with interactions between males of the same species or with mating behavior (Halloy and Castillo 2006). Some authors have suggested that these movements could indicate subordination when carried out slowly (“submissive wave”) and dominance when carried out quickly (“challenging wave”; Carpenter et al. 1970; Brattstrom 1971). Likewise, Vicente (2019) posits that forelimb waving could function as a social signal, as a submissive signal, or as a pursuit-deterrent signal in *Liolaemus pacha* (a species included in the *Liolaemus darwinii* group). Halloy and Castillo (2006) described forelimb waving in 11 *Liolaemus* species and they distinguished two types of movements: a simple movement which involves a single frontal extremity and a more complex movement which involves both frontal extremities. To complete this second complex movement, individuals lower their bodies to the ground and then lift both extremities with a circular waving movement. The latter was observed in *Liolaemus monticola* and *L. pictus*; the former, with more intense movements, was less frequent but was observed in the majority of the species, including *L. monticola*, *L. pictus*, *L. elongatus*, *L. cuyanus* (Halloy and Castillo 2006), and *Liolaemus loboi* (Martins et al. 2004). The tail movement consists of vibrations and horizontal movements of the tail (López and

Martín 2001, 2002; Trigosso-Venario et al. 2002; Aragón et al. 2006) and is usually associated with a behavior of submission or stress. This deployment may be accompanied by a dorsal flattening display, which implies a dorsal-ventral flattening of the body in such a way that the entire ventral surface is in contact with the substrate (Radder et al. 2006).

Another stereotyped behavior, specific to each species and common in some Patagonian lizards, is submersion in sand, inferred to be an escape behavior or preparation for periods of inactivity (Halloy 1995). This behavior has been described for *Liolaemus boulengeri*, *L. canqueli*, *L. cuyanus*, *L. darwinii*, *L. donosobarrosi*, *L. fitzingerii*, *L. grosseorum*, *L. melanops,* and *L. xanthoviridis* and for the sand dune lizards *Liolaemus wiegmannii* and *L. multimaculatus* (Halloy 2005; Kacoliris et al. 2009b), but it is present in all members of the *L. wiegmannii* group (e.g., *Liolaemus cuyumhue*; Fig. 11.1c). Though this behavior does have its particularities for each species (e.g., submersion time, tail movement, surface scratching, or smelling), in general these species first submerge their heads in the sand, pushing themselves with their hind limbs and placing their forelimbs along the length of their bodies, becoming invisible once their entire bodies are covered (Halloy 2005). Furthermore, behavioral characteristics, such as submersion in sand, provide information that can be used to reconstruct a phylogeny in and of themselves or together with other morphological, genetic, or ecological characteristics (Halloy et al. 2013). Based on 12 polymorphic characteristics of submersion behavior in 19 *Liolaemus* species belonging to the same monophyletic group (*L. boulengeri;* sensu Etheridge 1995), Halloy et al. (1998) defined three modes of submersion in sand: lizards that dig (slow), lizards that slither (medium), and lizards that dive into the sand (fast). This last behavior is the most efficient, and it is a characteristic behavior of lizards specialized in dune environments, like *Liolaemus multimaculatus* (Kacoliris et al. 2009a). The similarities within a group could indicate instances of adaptive convergence, while the differences in the modes of sand submersion (head/tail movements and time) in similar situations could reflect the effects of self-restrictions over the course of a species' life history (Halloy et al. 1998).

Lastly, two little-known but interesting behavioral displays are worth mentioning. One is the ocular protrusion observed in various species in captivity, among them *Liolaemus chiliensis* and *L. gravenhorstii*, which could be involved in ocular cleaning, a hypothesis only partially accepted (Reyes-Olivares et al. 2016), or as a thermoregulatory mechanism as it is commonly observed in lizards put through preferred temperature or critical maximum temperature experiments, as is the case with *L. parvus* and *L. ruibali* (first author personal observation). However, Reyes-Olivares et al. (2016) rule out the thermoregulatory hypothesis and propose that the eye-bulging might be modulated by other factors, mainly in conditions of captivity. The other is a distinctive cleaning behavior which has been recorded for a *L. tenuis* male that rubbed part of his head against the spines of the plant *Echinopsis chiloensis*. It would be interesting to study if this is a stereotyped behavior of the species and if it may be a way of cleaning residue or ectoparasites or a territorial behavior (Ramírez Alvarez 2015).

Within the communication behaviors, vocalization is fairly widespread in other groups of vertebrates, such as amphibians, birds, and mammals, but is less frequent in reptiles. However, studies and reports on acoustic communication in lizards do exist, mainly for Gekkonidae (Russell et al. 2000; Tang et al. 2001; Regalado 2003; Young et al. 2014; among others), some species of Leiosauridae (Frost et al. 2001; Labra et al. 2007b; Laspiur et al. 2007; Reyes-Olivares and Labra 2017), and isolated recordings of Liolaemidae (Carothers et al. 2001; Pincheira-Donoso 2002; Labra et al. 2013). In this sense, lizards respond to predators in diverse ways, among which vocalizations can be interpreted as signals of intimidation, warning, or stress, as well as calls for aid (Greene 1988; Carothers et al. 2001; Labra et al. 2016). In *Diplolaemus bibronii* and *D. sexcinctus*, distributed in the Patagonian steppe of Argentina and Chile, a sharp sound has been described as a violent expulsion of air when disturbed, accompanied by aggressive postures and tail movements, which would correspond to a distress call (Reyes-Olivares and Labra 2017). In *Phymaturus vociferator*, for example, two types of vocalizations were shown to be emitted. The first is a moderate sound, probably of guttural origin, for which lizards do not open their mouths. They make this sound when they are being manipulated or removed from their hiding places in crevices, that is, situations of prolonged stress. The second type of vocalization is similar to that recorded for *Leiosaurus* and *Pristidactylus* and is characterized by violent expulsions of air from a mouth which is completely open, producing a high-pitched whistle-like sound (Pincheira-Donoso 2002, 2004). This whistle is accompanied by an upright defensive posture with an open mouth and is produced in situations of sudden stress (Pincheira-Donoso 2002). On the other hand, in the genus *Liolaemus*, vocalization behaviors have been reported for *Liolaemus curis* (Núñez and Labra 1985) and the crying lizard *Liolaemus chiliensis* (Fig. 11.1d), probably produced by the larynx as an antipredatory response (Carothers et al. 2001). These lizards emit a sound when captured by a predator, which could warn conspecifics of the threat or create opportunities for escape (Labra et al. 2013). Conspecifics can reduce their risk of being captured by reacting to the cry with immobility or escape behaviors (Hoare and Labra 2013). Prolonged immobility reduces *L. chiliensis*'s possibility of being detected by its most frequent predators, the raptor *Falco sparverius* and the snake *Philodryas chamissonis*, as both employ a "sit and wait" hunting strategy, meaning that *L. chiliensis* reduces its risk by becoming immobile upon hearing the cry (Labra et al. 2016).

As will be mentioned in upcoming sections of this chapter, in the Patagonia region, lizard species are exposed to numerous predators, including arachnids, birds, snakes, and even other lizards. To cope with this situation, these lizards must utilize a variety of antipredatory strategies to reduce their risks of being captured, among which are tail autotomy; chemical, visual, and auditory communication; immobility; and/or escape. The initial escape distance (or critical distance), the escape latency, and the escape distance (distance from initial position to the closest shelter) have been used as indicators of lizards' predatory risk (Martín 2002; Kacoliris et al. 2009a; Cooper and Blumstein 2015; Fava and Acosta 2018). These critical and escape distances can be linked to individuals' weight, body temperature, and the perch height that saxicolous species select (Núñez 1996). For example, *Liolaemus curis* selects rocks at high altitude and as such has greater possibilities of seeing predators far away. Consequently, its initial escape distance is greater than that of the sympatric lizard *L. curicensis* that uses rocks at lower heights. Likewise, *L. curis* looks for shelter in the nearest microsites (least escape distance), while *L. curicensis* (Fig. 11.1e) prefers to use rocks as shelter or bushes if it is on the ground (Núñez 1996).

Escape behaviors can be affected by modifications in habitat structure, meaning vegetation coverage, as consequence of grazing, deforestation, and the introduction of new species of vegetation, among other causes (Amo et al. 2007; Anderson and Burgin 2008; Pietrek et al. 2009; Stellatelli et al. 2015). Two saxicolous species *Liolaemus elongatus* and *Phymaturus patagonicus*, inhabit the Patagonian steppe, both specialists in this habitat, along with *L. bibronii*, a versatile lizard in terms of ecological requirements and a generalist in the use of habitats (Scolaro 2005). Pietrek et al. (2009) compared these lizards in terms of their proportions of stops on uncovered ground in escape situations in experimental areas with different percentages of coverage. These authors observed that both *L. bibronii* and the specialist species made more stops on uncovered ground in situations with less vegetation coverage. In addition, all three species were captured more easily in this situation, though with *L. elongatus* and *P. patagonicus* being more susceptible than *L. bibronii*. Therefore, one of the costs associated with spread is an increase in predation risk, and in this sense low levels of vegetation coverage mean greater susceptibility to predation as exposure of the lizard is increased (Pietrek et al. 2009). On the other hand, an increase in vegetation coverage through forestation with non-native plants could also lead to changes in escape behaviors and could increase predatory possibilities (Stellatelli et al. 2015). In a study carried out in coastal dunes with both modified (non-native forestation) and natural (no forestation) habitats, Stellatelli et al. (2015) observed an increase in predatory pressure for lizards at the modified sites. Consequently, *Liolaemus wiegmannii* and *L. multimaculatus* make certain adjustments in their antipredatory behavior (Stellatelli et al. 2013, 2015). *Liolaemus wiegmannii*'s initial escape distance is greater at modified sites than at the non-forested sites, while *L. multimaculatus*'s initial escape distance is shorter at the modified sites, probably due to the fact that it employs a sand submersion strategy to reduce predation risks (Stellatelli et al. 2015).

The social behavior in lizards covers a great variety of behaviors, among which stand out parental care, reproductive courtship, cooperative care of offspring, custody behavior, aggressiveness, territoriality, and aggregation (Fox et al. 2003). The parental care can increase their offspring's physical aptitude by providing protection and/or nutrition, which in turn favors the survival of their descendants (Shine 1988; Somma 1990; Pike et al. 2016). The Patagonian region (north and south) implies rigorous environmental conditions for lizards, as well as great predatory pressure (see Sect. 11.3.2) and competition for resources. For this reason, parental care is an optimal strategy for guaranteeing the survival of one's offspring, a strategy that has been observed in some, generally viviparous, species of the family Liolaemidae (Halloy et al. 2013; Cabezas-Cartes et al. 2018a). In *Liolaemus elongatus,* females and their offspring occupy the same shelter for various days after birth, which provides to the newborn lizards thermal and hydrological stability during the cold, dry Patagonian nights (Halloy et al. 2007). It has also been observed that upon leaving the shelter, females of this species cover their newborn offspring, different from what has been recorded for *Phymaturus calcogaster* when females put their offspring on their backs; both behaviors probably serve to distract predators (Halloy et al. 2013). Two types of behaviors have been described when *Phymaturus spectabilis* females find themselves and their offspring under threat in experimental conditions (Cabezas-Cartes et al. 2018a). In the presence of a terrestrial predator such as *Pristidactylus nigroiugulus,* they display active behaviors such as headbobs, tail elevation, and escape, whereas when the threat is aerial, females reduce their activity and spend more time in crypsis near their offspring (Cabezas-Cartes et al. 2018a). Nevertheless, in field conditions in the Puna region, *Phymaturus williamsi* (non-Patagonian species) flees to nearby shelters when it detects the presence of a bird of prey and varies its time of reappearance depending on the size of the predator (Fava 2018; Fava and Acosta 2018). However, the similar behaviors observed in *Phymaturus* (Halloy et al. 2013) allow us to hypothesize a common pattern of parental care related to *Phymaturus*'s high reproductive investment (Cabezas-Cartes et al. 2018a).

One social behavior relatively unexplored in Patagonian lizards is aggregation. Alzamora et al. (2010) reported aggregation findings for *Phymaturus vociferator* in Laguna del Maule, Chile, in which they found 37 individuals, including males, females, juveniles, and newborns, under a single rock. This behavior could allow these lizards to survive the rigorous winter conditions of high-altitude environments (Alzamora et al. 2010) and is probably common for other *Phymaturus* species. A similar behavior has been frequently observed in several species of the *Phymaturus patagonicus* group as well as in species of the *Liolaemus elongatus* complex (Avila et al. unpublished, Fig. 11.2a). Clearly, the aggregation affects the thermoregulatory behavior of a lizard; however, the effect would not always represent an advantage for the individual. For example, in *Pristidactylus torquatus* and *Pristidactylus volcanensis,* the presence of conspecifics affects the thermoregulation of individuals, lizards which are solitary and territorial, and as such, social influence could be a factor involved in changes in body temperature (Labra 1995). Taking into account Patagonia's extreme environmental conditions, with low temperatures and snowfall in winter and great thermal amplitude during the lizards' active seasons, it would be interesting to evaluate aggregation behaviors in other Patagonian species as a strategy for coping with these extreme conditions.

The recognition of familiar individuals, primarily in territorial species, is a social behavior that could help to reduce the frequency and intensity of aggressive encounters, stabilizing social systems and reducing the costs of preserving territory (Fox and Baird 1992; Hanley et al. 1999; Vitt and Caldwell 2013). For example, *Liolaemus tenuis* males are territorial and tend to tone down their aggressive behavior in the presence of a familiar individual as opposed to an unknown conspecific (Trigosso-Venario et al. 2002), responding to the "dear enemy" phenomenon (Ydenberg et al. 1988). Likewise, recognition of a familiar individual is lost after a prolonged period of time without social interaction, which is relevant for interactions with "floating"

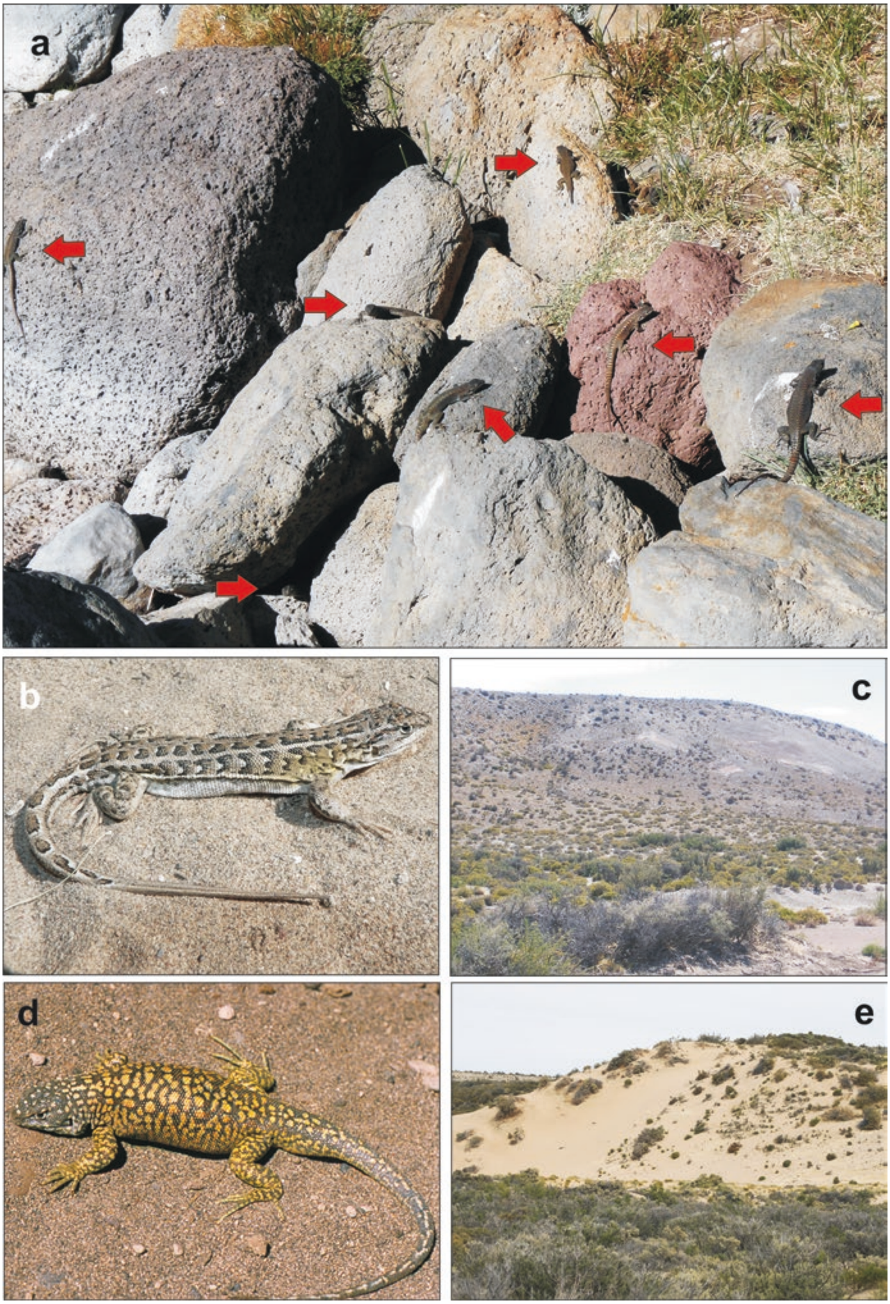

Fig. 11.2 (**a**) Aggregation of *Liolaemus elongatus* at the Area Natural Protegida Tromen, Neuquén, Argentina. Red arrow marks adult individuals (courtesy of Daniel Paz Barreto). (**b**) *L. inacayali*, male. (**c**) Habitat of *L. inacayali* near the type locality, in Río Negro Province, Argentina. (**d**) *Liolaemus xanthoviridis*. (**e**) Habitat of *L. xanthoviridis* at Isla Escondida Bay, Chubut, Argentina

males or neighbors who lose their territory and later attempt to fight to recover it (Trigosso-Venario et al. 2002).

11.2.2 Use of Time and Space

A fundamental aspect in lizard ecology is related to the different ways in which species make use of spatial and temporal resources (Reilly et al. 2007). Knowledge of the rhythm of temporal, daily, and seasonal activity, together with the use of space, can provide details about the behavior, thermal requirements, and thermoregulatory mechanisms of a species (Chap. 13); a large part of the activity of any organism depends on the thermal characteristics of its environment (Labra et al. 2001c; Smith and Ballinger 2001; Villavicencio et al. 2002; Kacoliris et al. 2011). Likewise, knowledge of the use of space is important because in this way we understand the resources potentially available to lizards, such as food, water, mates, thermal availability, nesting sites, and shelters, among others (Begon et al. 1990; Pough et al. 2001). That is, lizard species perform movements and select sites that optimize their subsistence, survival, and reproduction (Pough et al. 2001; Kacoliris et al. 2011; Vitt and Caldwell 2013).

Patterns of daily and seasonal activity of species that inhabit the Patagonian plateau are limited to months with suitable temperatures. Most of the Patagonian lizards are limited to the spring and summer months, from September to March, while between April and August, they are in a period of hibernation. But in Peninsula Valdés, *Liolaemus gracilis* and other *Liolaemus* (probably *L. darwinii* and *L. melanops*) have been observed in July or August. Winter activity in Patagonian lizards could be more common than expected but is an issue not studied until now. Among the species for which characteristics of population structure are known, we find *Liolaemus inacayali* (Fig. 11.2b) present in an ecotone zone between Patagonian steppe and the Monte, in Río Negro Province. This region is characterized for its dry, desert climate; an average annual temperature of 4 ° C; absolute minimum and maximum temperatures of 1 ° C and 10 ° C, respectively; annual precipitations of less than 200 mm (mostly snowfall); and winds out of the west at 100 km/h. This species remains active from mid-September, the end of the southern winter, until March, the beginning of autumn. The first age group to emerge from its winter lethargy are the juveniles, born the previous season. Later, adult males and females appear. Births take place in February, adult activity declines, and youths remain active, with this last group being the last to retire at the beginning of autumn (Acosta et al. 1996). The microenvironment mainly utilized by *L. inacayali* adults is the sand base of bushes, used as a site for feeding, protection, and the digging of caves for shelter, in addition to small rocks (Fig. 11.2c). This species is rarely found in rocky areas; nevertheless, young individuals can be found in areas with little or no vegetation coverage. Their daily activity is unimodal and they are heliothermal. This species shares its habitat with two other species, *Liolaemus bibronii*, with a lower population density living along the edges of the plateau, and *Leiosaurus belli*, also found in the sand base of bush plants, though without temporal overlap (Acosta et al. 1996).

Liolaemus xanthoviridis is another Patagonian species distributed around the Plateau of Montemayor, in Chubut Province, Argentina. The period of activity of these arenicolous lizards begins in late September to early October and continues until mid- to late March (depending on environmental temperature). Between October and December, matings and oviposition of eggs occur, while between January and March, the emergence of the first juveniles marks the moment that the hatching occurs. For *Liolaemus xanthoviridis,* the vegetation cover would be of great importance at the time of using a particular microhabitat, since the microhabitat that it occupies presents on average 68% of total vegetation cover (Escudero 2016) (Fig. 11.2d).

Another species that inhabits the Patagonian plateau is *Homonota darwinii* (Fig. 11.3a), the most southerly nocturnal lizard in the world. Due to the harsh climatic conditions prevailing in the region, adequate shelter is limited. The performance and survival of nocturnal lizards depends on the thermal quality of their diurnal shelter. A study of this gecko's use of shelter shows that shelters with higher temperatures were always selected, independent of the rocks' size or thickness. These results demonstrate the importance of a shelter's thermal quality for reptiles living in extreme environments (Aguilar and Cruz 2010). It is very difficult to find *H. darwinii* in natural environments, but instead it is very easy to find them in garbage (Fig. 11.3b), building debris, or even shorebirds remains (Fig. 11.3c), or trapped with other lizards species, in artificial ponds made by oil extraction companies (Fig. 11.3d).

It seems that the only *Liolaemus* species with occasional nocturnal activity in cold regions of the Patagonian Andes is *L. tenuis* (Avila and Morando 2015) (Fig. 11.3e), a lizard widely distributed in central Chile, though in Argentina it only inhabits a small area of Andean-Patagonian forest in the province of Neuquén. Other species of *Liolaemus* are only active for a brief period at dusk in the Monte region. However, the vast majority of *Liolaemus* lizards have daytime activity, with bimodal patterns (activity in the morning and afternoon, e.g., *L. lemniscatus*, *L. monticola*, *L. tenuis*) or unimodal patterns (activity from midmorning to early afternoon), as is the case for *L. schroederi* and most of the species of the Teiidae family that peak at the hot middle of day (Pianka 1969; Fuentes 1976; Belver and Avila 2001).

The wide diversity and versatility of species in *Liolaemus* allow us to identify different types of microhabitats selected by lizards, such as rocks (e.g., *L. monticola*, *L. curi, L. nitidus*), trunks and trees (e.g., *L. tenuis, L. pictus*), open ground (e.g., *L. lemniscatus*, *L. curicensis*), under shrubs (e.g., *L. schroederi*, *L. chiliensis*), and sand dunes (e.g., *L. multimaculatus*, *L. cuyumhue*), among others (Fuentes 1976; Jaksić and Fuentes 1980; Núñez 1996; Avila et al. 2009; Kacoliris et al. 2011). Additionally, Zúñiga et al. (2016) carried out a study in central-southern Chile in which they compared the habitat use of three lizard species, *L. tenuis*, *L. pictus,* and *L. lemniscatus*, in native forests and plantations of *Eucalyptus globulus*, and they evaluated niche segregation at the microhabitat level. They observed

Fig. 11.3 (**a**) *Homonota darwinii* with broken and regenerating tail in natural environment. (**b**) Human garbage used as shelter by *H. darwinii*. (**c**) *H. darwinii* (red arrow) living in a carcass of a dead shorebird in Playa Colombo, Península de Valdés (courtesy of J. Grummer). (**d**) Dead lizards trapped in oil rig artificial pond. (**e**) *Liolaemus tenuis* foraging around a patio light in the night (Avila and Morando 2015). (**f**) *Lycium* fruits, a common food for some lizard species (courtesy of C.H.F. Pérez). (**g**) *L. austromendocinus* eating a butterfly in a rocky outcrop near Crucero Catriel, Neuquén, Argentina (courtesy of C.H.F. Pérez). (**h**) *L. grosseorum* eating a scorpion in the Bajo de Añelo, Neuquén Province, Argentina (courtesy of M.V. Brizio)

higher frequency in the native forest as opposed to the plantations. The three species make a differential use of microhabitats; *L. tenuis* is more associated with trees, *L. lemniscatus* with the ground level, and *L. pictus* with a generalist tendency (Zúñiga et al. 2016).

An individual's preference for a particular microhabitat can affect how it perceives predation risk and therefore its antipredatory behavior (Constanzo-Chávez et al. 2018). The sympatric species *Liolaemus chiliensis* and *Liolaemus nitidus* select different microhabitats and may experience different selective pressures against shared predators (e.g., raptors and snakes). On the one hand, *L. chiliensis* is commonly found basking on bushes, a complex microhabitat that can provide protection against predators, and only reduces its activity in high-risk conditions, while *L. nitidus* prefers open microhabitats at the top of rocks with high exposure to visual predators such as raptors. In this sense, *L. nitidus* reduces its activity and is alerted to a high or low risk of predation (Constanzo-Chávez et al. 2018). Similarly, *Liolaemus curis* (exclusively saxicolous) and *Liolaemus curicensis* (terrestrial-saxicolous), which inhabit a mountain sector with a Mediterranean climate and fluctuating rains where vegetation is squat and xeromorphic, use shelter differently in the presence of predators; *L. curi* flees into crevices, while *L. curicensis* uses bushes for cover. These species are not syntopic but rather allotropic. They live in different spaces and coexist, thanks to their habitats, *L. curis* being restricted to large rocks and *L. curicensis* to small bushes with isolated rocks (Núñez 1996).

In Tierra del Fuego, the world's southernmost region, lives *Liolaemus magellanicus*, in two areas that differ in their appearance, vegetation, and soil, though both are located less than 200 m from the coast. The vegetation at one of the sites is coastal brush with few bushes and plants in thickets. The soil is sandy and dug up by the fossorial rodent *Ctenomys magellanicus* (Ctenomyidae). The other site is a coastal steppe homogeneously covered by *Festuca* sp. grass. Its soil is a sandy-clay mix and fossorial rodents are not present. At the first site, *L. magellanicus* individuals were seen at the entrance of *Ctenomys* dens, and at the second site below debris (Jaksić and Schwenk 1983).

The local spatial distribution of individuals is often described in terms of "home range" (HR) and "territory." The first is defined as the entire area in which an individual performs its daily activities, which includes exploratory movements outside of it and in which it spends most of the time and is not necessarily exclusive or defended (Burt 1943), whereas "territory" is a defended area for exclusive use (Noble 1939; Brown and Orians 1970). Few studies have examined space use in Patagonian species of lizards. In this sense, the Patagonian *Liolaemus melanops* was studied, a medium-sized lizard (90 mm snout to vent length) which is found in low sandy zones and coastal dunes of the provinces of Río Negro and Chubut, Argentina. The study was carried out with a population located in center of Chubut, with no significant differences in average HR for males and females. Moreover, no correlation between body size and the size of the HR was found, though great overlap in the HR utilized by males was observed; this was not the case for females (Frutos and Belver 2007). *Liolaemus petrophilus* presented a similar average home range in males and females with a high degree of inter- and intrasexual overlap. This important degree of overlap would seem to indicate the lack of territoriality in males and females (Frutos 2009). Opposite results were recorded in a coastal species, and males and females of *L. xanthoviridis* used space differently. Males presented home ranges associated with body size and greater than females. The observed overlapped patterns could indicate that females are territorial, but not males (at least with respect to the complete HR; Escudero 2016). On the other hand, in the Andean cordillera of central Chile, a study on the use of space in populations of seven *Liolaemus* species suggested that the high-elevation lizards (2900 msnm; *L. belli*, *L. leopardinus*) were tolerant of high home range overlap of conspecifics, both males with males and females with females; they found no evidence of territorial social organization. Lizards from low (1200 msnm; *L. monticola*, *L. lemniscatus*) and mid (2300 msnm; *L. schroederi*, *L. nitidus*) elevation sites generally were aggressive; males were intolerant of home range overlap with other males, and females also showed low spatial overlap. These species showed territorial social organization (Fox and Shipman 2003).

11.3 Trophic Ecology

11.3.1 Diet

Knowledge of trophic ecology, particularly diet, has important implications for our understanding of reptile ecology in general and their functional morphology, ecomorphology, behavior, and physiology. At the same time, in lizards there exist diverse sources of variation in diet due to hereditary features such as body size, biomechanics, activity time, resource availability, sensory abilities, thermoregulation strategies, modes of foraging, and physiological restrictions, among others (Vitt et al. 1997; Vitt et al. 2003; Vitt and Pianka 2007). The description and quantification of diet are principal aspects of studies of a species' ecology (Pianka 1973; Aun et al. 1999; Vitt and Pianka 2007) and are closely related to the availability and abundance of food resources, inter- and intra-species competition, capture abilities, and habitat conditions (Aun et al. 1999; Castro et al. 2013). Studies on what makes up a species' diet have been carried out using a variety of methodologies, which include direct observation of foraging in the field and stomach and feces analysis. Nevertheless, it has been demonstrated that direct observation of stomach and intestinal contents is considerably more precise for the determination of diet than feces observation (Pincheira-Donoso 2008) and field observations, which are often coincidental and random.

In the Argentine and Chile Patagonia, studies of the trophic aspects of lizard species are particularly limited. We only have general data about their trophic niche, taken from notes of particular findings, from some more specific works on diet, and from anecdotal data on natural history in the species' description. Diet composition has only been reported in detail for 21 species (11.04%) of Patagonian lizards, the majority of which are carnivorous (insectivores) and/or omnivorous (Table 11.1).

Table 11.1 Items recorded in the diet of Patagonian lizards

	Arthropods							Chordates			Plant matter				
Species	Insecta	Diplopoda	Chilopoda	Arachnida	Isopoda	Entognatha	Mollusca	Reptile	Bird	Mammal	Fruit	Seed	Flower	Others	Diet
Liolaemus bibronii[a]	★			★							★	★	★	★	Insectivore/ Omnivore
Liolaemus burmeisteri[b]	★			★											Insectivore
Liolaemus crandalli[c]	★											★	★		Omnivore
Liolaemus curicensis[d]	★			★							★	★		★	Omnivore
Liolaemus curis[d]	★			★		★					★	★	★	★	Omnivore
Liolaemus cuyanus[e]	★			★							★	★	★	★	Omnivore
Liolaemus cyanogaster[f]	★			★											Insectivore
Liolaemus darwinii[g]	★			★											Insectivore
Liolaemus elongatus[h]	★			★								★		★	Omnivore
Liolaemus inacayali[i]	★										★	★	★	★	Omnivore
Liolaemus lemniscatus[d]	★		★	★			★								Insectivore
Liolaemus monticola[j]	★			★								★	★		Insectivore
Liolaemus nitidus[k]	★	★													Insectivore

(continued)

Table 11.1 (continued)

Species	Arthropods						Mollusca	Chordates			Plant matter				Diet
	Insecta	Diplopoda	Chilopoda	Arachnida	Isopoda	Entognatha		Reptile	Bird	Mammal	Fruit	Seed	Flower	Others	
Liolaemus pictus[l, m]	★			★		★	★								Insectivore
Liolaemus wiegmannii[n]	★			★											Insectivore
Phymaturus vociferator[o]	★										★	★			Herbivorous
Phymaturus zapalensis[p]	★													★	Omnivore
Salvator rufescens[q]	★		★	★	★		★	★	★	★	★	★			Omnivore
Teius oculatus[r]	★			★	★										Insectivore
Homonota darwinii[s]	★			★											Insectivore
Homonota horrida[t]	★			★											Insectivore

Data were selected from published sources

References; [a] Belver and Avila (2002); [b] Avila et al. (2012); [c] Avila et al. (2015); [d] Núñez (1996); [e] Moreno Azócar and Acosta (2011); [f] Codoceo (1954); [g] De Viana (1994); [h] Quatrini et al. (2001); [i] Acosta et al. (1996); [j] Ipinza Regla (1985); [k] Jaksić and Fuentes (1980); [l] Ortiz (1974); [m] Vidal (2007); [n] Aun et al. (1999); [o] Celedón-Neghme et al. (2005); [p] Boretto and Ibargüengoytía (2018); [q] López Juri et al. (2015); [r] Acosta et al. (1991); [s] Kun et al. (2010); [t] Aun and Martori (1994)

Some anecdotical data is available from occasional field observations, for example, for *L. austromendocinus* (Fig. 11.3g) or *L. grosseorum* (Fig. 11.3h). In general for *Liolaemus* species, their predominant prey are arthropods, and within this group, the Formicidae family, as several species have been observed eating ants. Ants represent a resource widely available in large densities, reason for which many lizard species choose to exploit them utilizing an active search strategy. The energy cost that this strategy demands is compensated for by the ease of trapping this prey and by its abundance (Quatrini et al. 2001). The diet composition of only one herbivorous species, *Phymaturus vociferator*, is known and includes fruit and vegetation matter, including seeds, and on occasion ant remains (categorized as incidental). This species demonstrates a clear tendency for the consumption of fruits, mainly those of *Calandrinia* sp. (Celedón-Neghme et al. 2005), as opposed to what has been reported for non-Patagonian *Phymaturus*, such as *P. williamsi,* which mainly consumes flowers from the genus *Adesmia,* or *P. punae,* which prefers *Adesmia* stems and leaves (Castro et al. 2013; Córdoba et al. 2015). On the other hand, Boretto and Ibargüengoytía (2018) reported for *Phymaturus zapalensis*, endemic to Laguna Blanca National Park in Neuquén Province, presence of plant matter and insects in the digestive tract of 15 individuals, indicating an omnivorous diet unique in the genus. Boretto and Ibargüengoytía (2018) suggest that a high-energy omnivorous diet could explain an annual reproductive cycle in females of *P. zapalensis*, instead of the characteristic biennial cycle in other species of the genus (Boretto and Ibargüengoytía 2009; Boretto et al. 2018; Castro et al. 2018).

Of the 169 taxa present in the Patagonia region, the great majority (75%) are classified as insectivorous or insectivorous/omnivorous, while strictly herbivorous species are considerably less common, reserved almost exclusively for species of the genus *Phymaturus* and some *Liolaemus* species, such as *L. avilai*, *L. morandae* (Breitman et al. 2011), *L. ceii* (Scrocchi et al. 2010), and *L. silvanae* (Abdala 2012), though serious studies are needed to corroborate this data. A tendency toward herbivorism has been documented for small lizards in cold climates (Espinoza et al. 2004). The availability of animal resources could fluctuate and become limited during certain times of the year in variable and hostile environments such as steppes, the Patagonian coast, and Andean locations which are volcanic and rocky. This implies an additional energy cost in the search for prey. In these cold and variable environments, the use of vegetation resources, which are more stable throughout the year, would be a good foraging strategy. However, herbivorism has additional costs for digestion, as the majority of the energy contained in vegetation matter is in the form of fibrous compounds, such as cellulose. For this reason, herbivores have intestinal specializations that include blinds, intestinal valves, and nematodes in the rear intestine which facilitate the fermentation of fiber components and lengthen digestion retention time, thereby increasing digestive efficiency (Iverson 1982; Stevens and Hume 1998; Castro et al. 2013).

The strategies employed by lizards in their search for food involve ways of obtaining matter and energy needed for growth, maintenance, and reproduction. But this search for food implies both energy and survival costs, because when a lizard is feeding, it may be exposed to predators and because time dedicated to feeding means time not invested in other activities such as courtship. As such, the foraging strategies that a species employs must be optimal in terms of energy returns (Pianka 1966; Huey and Pianka 1981). Two strategies of food acquisition have been described. In the first, known as the "sit and wait" strategy, the predator waits in a certain location until its prey passes nearby and then "ambushes" the prey. In this case, the energy that an individual requires is little, and an energy gain will depend on the density and mobility of its prey. On the other hand, in the "active foraging" strategy, the predator actively seeks out its prey and as such requires greater energy for the search but is not dependent on the density and mobility of its prey (Pianka 1966). Generally speaking, a generalist and opportunist diet is associated with the "sit and wait" method, while a specialist diet is more closely related to the "active foraging" strategy, as is the case of the majority of species from the Teiidae family, which are frequently observed looking for food between patches of vegetation, digging through fallen leaves and into the ground and sticking their snouts into holes or caves (Acosta et al. 1991). Nonetheless, both of these tactics are the extremes on a continuum of possible strategies for food location, strategies that versatile and opportunistic species like those of the genus *Liolaemus* make use of. Within this group, we observe both generalist (*Liolaemus curicensis, L. lemniscatus, L. tenuis, L. schroederi*) and specialist species (*L. curis, L. monticola*) in terms of diet, who employ a "sit and wait" method of foraging (Fuentes 1976; Núñez 1996), to the employment of mixed foraging strategies, as those utilized by *Liolaemus wiegmannii*, *L. bibronii*, *L. inacayali,* or the gecko *Homonota horrida* and *H. darwinii*, depending on available resources (Aun and Martori 1994; Acosta et al. 1996; Aun et al. 1999; Belver and Avila 2002; Kun et al. 2010). These changes in feeding behavior can be interpreted to be adaptations to the variability of food resources in the highly unpredictable desert environment, that is, the arid, cold Patagonian steppe, and could favor species with an opportunistic diet in the southern region (Belver and Avila 2002).

Likewise, lizard foraging strategies, diet, and availability of resources also probably vary due to the influence of extrinsic factors such as the seasons and temperature of the environment. As such, it is essential to carry out long-term, annual studies in order to take into account opportunistic changes in species' trophic ecology. Additionally, intraspecific differences (sex and age group) in diet may also exist, as well as among populations of the same species. For this reason, it is necessary to look at these factors in order to have a greater understanding of a species' biology. Studies that evaluate seasonal and intrapopulation changes are limited or nonexistent for Patagonian lizard species. For example, differences in diet composition between age groups and seasons have been observed in *Liolaemus inacayali*. During the spring, juveniles mainly feed on ants and vegetation, while in the summer, their diet is restricted to Diptera and Hymenoptera, and in second place ants. Adults (both males and females) mainly consume vegetation and ants during the first period, while during the second period, Hemiptera become more relevant and vegetation consumption decreases. This age group and seasonal variation is associated with the variation in abundance of food offer on site; for instance, greater consumption of vegetation in the first period could possibly be due to a lower abundance of arthropods during this time (Acosta et al. 1996). The *Liolaemus pictus* diet is mainly made up of Diptera, Homoptera, Hymenoptera, and Coleoptera, and its composition does not vary among populations at three different sites of the Vicente Pérez Rosales National Park in Chile. This coincides with what Vidal (2007) proposed, although there are variations between locations: *L. pictus* consumes preys in relatively similar quantities in different populations (Vidal and Labra 2008). Nevertheless, the adults of these populations have a higher preference for Coleoptera and arachnids than juveniles (Ortiz 1974). In addition, *L. pictus* has been considered an active forager with an opportunistic diet since it consumes a wide variety of large-size species (19 items; Vidal 2007; Vidal and Labra 2008), similar to the food behavior documented for *L. lemniscatus* (16 items; Núñez et al. 1989).

For two populations of *Liolaemus elongatus*, one at a forest site and the other at a plateau site, Quatrini et al. (2001) did not observe qualitative differences in diet. Both populations are omnivorous, with ants being the fundamental dietary component. They only differ in their second item of importance, Homoptera for the plateau population and seeds for the forest population, as fruits are widely available at that site. Another study on trophic diversity in sympatric species (*Liolaemus lemniscatus*, *L. tenuis*, *L. fuscus*) and different populations of *L. lemniscatus* proposes that interspecific and population variations in diet are determined by variation in the availability of trophic resources, which in turn determines a specialized or generalist diet (Hurtubia 1973). Therefore, geographical variations in biotic and abiotic characteristics can determine populations' variations in predators (Vidal and Labra 2008).

Changes in diet composition between sexes may be due to a decrease in mobility for females during the gestation period (Martori and Aun 1997). As an example, Aun et al. (1999) observed that ants for *Liolaemus wiegmannii* are generally an important component of the diet. However, in the spring, females mainly feed on flies, probably due to the fact that gestation restricts their range of activity to shelter walls, while males, in addition to consuming ants, feed on locusts that they find by roaming about the territory. They also observe that in the winter the secondary prey for females is spiders, which are sedentary, while for males, larvae are important resources for biomass contributions (Aun et al. 1999). Another source of variation in diet, a source that has not been well explored, is the length of the lizard and its head shape. Jaksić and Fuentes (1980) observed that the most abundant prey in the *Liolaemus nitidus* diet are Coleoptera and found that there is a positive association between an individual's length and the length of the consumed prey. They argue that larger individuals have larger snouts that allow them to trap and swallow larger prey. There is also a correlation between the variety of prey consumed and lizard size, as although they do prefer larger prey, they do not stop feeding on smaller prey as well, such as ants. On the other hand, bigger lizards tend to be omnivorous-herbivorous as it is energetically more beneficial for them to feed on small insects (Pough 1973; Moreno Azócar and Acosta 2011), in addition to the fact that the availability of bigger preys is usually limited (Fuentes 1977; Jaksić and Fuentes 1980). Hence, as *L. nitidus* individuals grow, there is a tendency toward herbivorism because as juveniles the availability of small prey in relation to their size is abundant on site, but this is not the case for adults (Jaksić 1978; Jaksić and Fuentes 1980).

As can be seen in the examples presented, diet composition and availability of resources are influenced by various intrinsic and extrinsic factors, a fact which justifies the need for studies that fill in information gaps regarding the trophic ecology of Patagonian lizards. Moreover, the methodological designs of these studies should take into account random factors such as seasonality, environment type, sex, and ontogeny, among others, so as to obtain a greater generalization and understanding of the ecological patterns of species in this region.

11.3.2 Predation and Seed Dispersal

From a functional point of view, lizards can be considered fundamental elements of their ecosystems, participating in processes central to the functioning of natural systems, including seed dispersal and pollination, as well as acting as prey for other groups such as raptors, snakes, and other lizards, among others (Acosta et al. 2018). In this sense, seed dispersal is an important part of a plant's life cycle, in which animals may play a determining role as biological interactions between plants and animals could occur and both could benefit. In his review, Godínez-Álvarez (2004) indicates that various species of lizards feed on nectar and fruits and that upon consuming these materials, they could be effectively pollinating flowers or dispersing seeds to sites far from the mother plant. Frugivorous species not only play an important role in seed dispersal; they also have an important impact at the moment of germination, depending on how the seed passes through the lizard's digestive tract (Traveset and Willson 1997; Varela and Bucher 2002). *Teius teyou* is considered a legitimate disperser of viable seeds from the *Ziziphus mistol* plant, as the seeds begin to germinate a few months after passing through the digestive tract. Nevertheless, the greatest benefit this plant receives from having its seeds ingested by *T. teyou* is seed dispersal, demonstrating a "high-quality deposit pattern" (Schupp 1993; Varela and Bucher 2002). Willson et al. (1996) documented frugivorism and seed transport for *Liolaemus pictus*, a species that is mainly described as arboreal. In the analysis of its feces, both *Nertera granadensis* and *Relbunium hypocarpium* seeds are found, and in the case of *Nertera,* the seeds germinated faster after passing through the lizards' digestive tract.

Several studies have emphasized the importance that omnivorous or herbivorous lizards have in the dispersal process, as fleshy fruits constitute a large part of their diets (Fellers and Drost 1991; Valido and Nogales 1994). Without doubt, *Phymaturus* species, saxicolous and herbivorous, are excellent potential seed dispersers. In the feces of *Phymaturus vociferator*, seeds from three species of plants are found: *Berberis empetrifolia, Rumex acetosella,* and *Calandrinia* sp. from the Laguna La Laja National Park in Chile. Studies carried out by Celedón-Neghme et al. (2005) demonstrate that *P. vociferator* has a clear preference for the consumption of *Calandrinia* sp., while at the same time the percentage of germination and viability for *B. empetrifolia* seeds is higher after having passed through the digestive tract. In addition, *P. vociferator* disperses seeds from the mother plant in an average area of

~20.75 m^2, for which this lizard can be considered a legitimate disperser of these plants. Though there are no additional studies on the diet and seed dispersal of other *Phymaturus* species in Patagonia, it is likely that this numerous group of herbivorous lizards, together with other omnivorous and herbivorous *Liolaemus*, have a fundamental role as seed dispersers in the structure and diversity of vegetation in the Patagonia region, at least on a local scale in fragile Andean-Patagonian environments. Several *Phymaturus* species (*P. camilae*, *P. verdugo*) have been observed by the authors eating fruits of *Lycium* spp. (Fig. 11.3f) and *Berberis microphylla* (Pérez, personal communication), and it is common to observe some seeds in recent feces of species of this genus, but no studies on this issues have been carried out.

On the other hand, in Patagonia's natural systems, saurophagy is common in many large species, mainly lizards from the Leiosauridae family, among them *Diplolaemus darwinii* (Pérez et al. 2009a) (Fig. 11.4a). Nevertheless, it has also been documented in *Liolaemus* species that coexist in sympatry, as is the case of syntopic *L. bibronii* with *L. petrophilus* and *L. austromendocinus*. They are often observed occupying the same microhabitats. For these last two species, juvenile and adult of *L. bibronii* have been reported as items of prey (Avila and Morando 2002; Pérez et al. 2009b). Another example is *Homonota underwoodi*, in whose stomach contents a juvenile of *L. darwinii* was found (Blanco et al. 2012). Within saurophagy, cannibalism may also exist and in the majority of cases these predatory strategies appear as opportunistic and as a result of normal predatory behavior (Polis and Myers 1985). Reports of cannibalism exist for *Aurivela longicauda*, *Liolaemus rothi* (Fig. 11.4b), *L. darwinii*, *L. chiliensis*, *L. baguali,* and *Diplolaemus leopardinus* (Scolaro 2005; Pincheira-Donoso 2000; Ripoll and Acosta 2007; Kozykariski et al. 2009; Blanco et al. 2012).

Lizards are also part of interspecies predator-prey relationships with other groups of animals, where various lizards, among them *Liolaemus goetschi*, *L. lineomaculatus*, *L. fitzingerii*, *L. cyanogaster, L. chilensis, L. fuscus*, *Leiosaurus belli, Pristidactylus torquatus*, *Diplolaemus bibronii*, *Homonota darwinii*, *H. underwoodi*, *Aurivela longicauda*, *Teius teyou,* and others, are often the prey of different predators such as birds (*Geranoaetus polyosoma* (common hawk), *Athene cunicularia* (burrowing owl) (Fig. 11.4c), *Bubo magellanicus* (Magellanic horned owl), *Falco sparverius* (American kestrel) (Fig. 11.4d), *Falco femoralis* (aplomado falcon), *Pseudoseisura gutturalis* (Cacholote), *Agriornis montana* (black-billed shrike-tyrant), and *Leistes loyca* (common meadowlark) (Fig. 11.4e)), snakes (*Philodryas chamissonis, Phylodrias psammophidea, Tachymenis chilensis, Bothrops ammodytoides*), and arachnids (*Lycosa polyostoma* (wolf spider), *Bothriurus burmeisteri*, *Tymogenes* sp. (scorpion) (Fig. 11.4f), and others (Greene 1992; Trejo et al. 2003; Figueroa Rojas et al. 2004; Pérez and Avila 2005; Udrizar Sauthier et al. 2007; Pérez et al. 2009a, b, 2010; Santillán et al. 2009; Avila and Pérez 2011; Bianchini 2014; Pérez and Minoli 2014; Avila et al. 2017; Galdeano et al. 2017; Gómez Alés et al. 2017a; Udrizar Sauthier et al. 2017)). As such, lizards are of utmost importance to trophic networks as essential components of ecosystem processes (Acosta et al. 2018) in the Patagonia region.

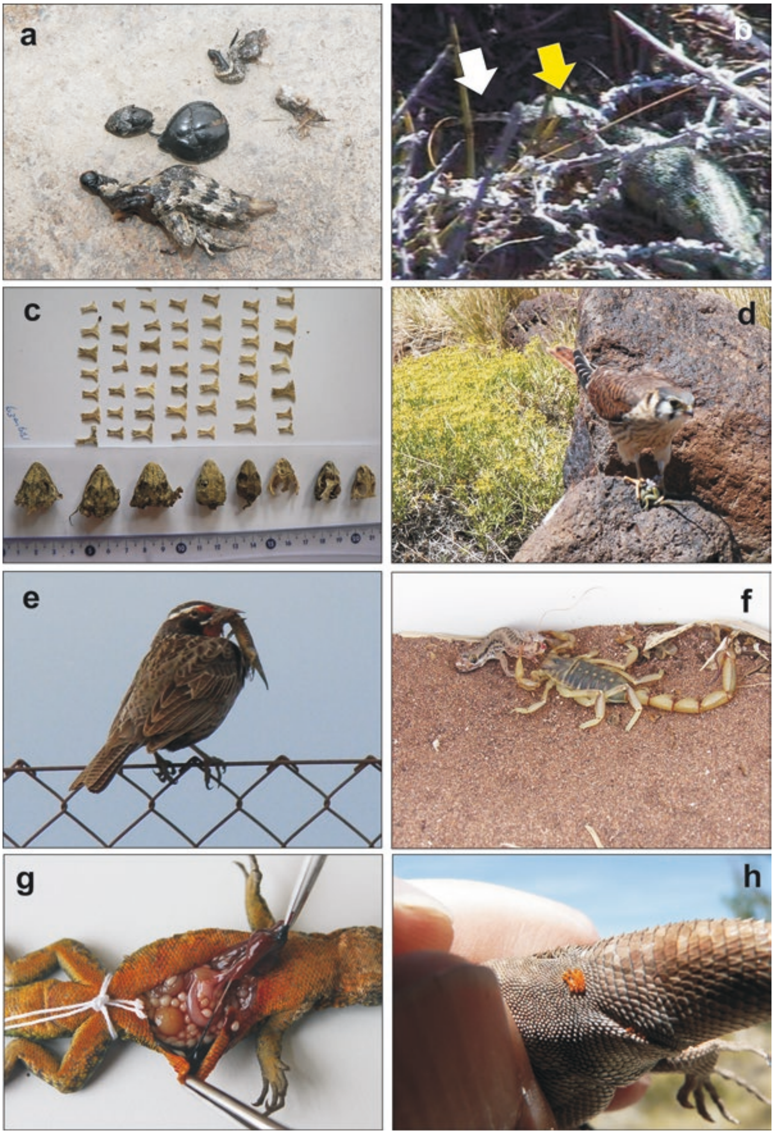

Fig. 11.4 (**a**) Remain of a *Liolaemus* lizard hunted by a *Diplolaemus darwinii* (courtesy of C.H.F. Pérez, Pérez et al. 2009a). (**b**) Cannibalism in *L. rothi* (courtesy of M. Kozykariski, Kozykariski et al. 2009). (**c**) Bone remains of *Leiosaurus belli* found around a burrowing owl (*Athene cunicularia*) nest (Udrizar Sauthier et al. 2007). (**d**) *Falco sparverius* eating a *Liolaemus elongatus* lizard in the Area Natural Protegida Tromen (courtesy of D. Paz Barreto). (**e**) *Leistes loyca* with a *L. multimaculatus* near El Condor Beach, Río Negro Province, Argentina (courtesy of M. Bianchini, Bianchini 2014). (**f**) *Tymogenes* spp. eating a *Homonota underwoodi* in the Bajo de Añelo, Neuquén, Argentina (courtesy of M.V. Brizio). (**g**) Unidentified internal parasites in *Liolaemus pictus*. (**h**) Thicks in femoral pocket in *L. austromendocinus*

11.4 Parasitism

Parasitism is one of the most common styles of life in the animal kingdom and is widespread within natural ecosystems (Castillo et al. 2018). Knowledge of parasitic relationships between hosts, such as lizards, and different types of parasites (mites, ticks, helminths, and nematodes, among others) is important both from an ecological point of view and in terms of host health, as these relationships can hinder important physiological processes, such as thermoregulation, digestion, and immune response (García-De la Peña et al. 2010; Vitt and Caldwell 2013; San Martín-Órdenes et al. 2019). Likewise, parasites are good ecological indicators and provide information on phylogenetic relationships with their hosts (Cruz Reyes 1993). Moreover, the alteration of habitats due to anthropic actions can generate physiological stress for some species, creating nutritional variations and the appearance of opportunistic parasite species. In this sense, the absence or presence of certain parasites can be indicators of host stress, which could reflect certain environmental changes (Brooks and McLennan 1991; Accattoli and Salazar Martínez 2012).

Negative effects that parasitism could cause include anemia and a decrease in performance, followed by a reduction in survival, competitiveness, thermoregulation, social interactions, the ability to attract mates, and, in the case of females, fertility (Vitt and Caldwell 2013). On the other hand, the presence of certain nematode endoparasites in the intestines of herbivorous lizards is common and is not necessarily a detrimental factor for the host, as these parasites can help with the decomposition of cellulose in the diets of these lizards (Jaksić and Fuentes 1980; Iverson 1982; Stevens and Hume 1998; Carothers and Jaksić 2001). Therefore, parasitism can be interpreted as a process of selection that affects the ecology, physiology, evolution, and life histories of its hosts (Vitt and Caldwell 2013).

The majority of works referring to parasitism in Argentina and Chile are limited to the description of species or isolated recordings of infestations (Table 11.2). Few studies aim to understand how a parasite can affect a host's survival or what its relationship is to body conditions, sex differences, or the existence of seasonal variations (climate and reproductive conditions), with respect to the prevalence and intensity of parasites on a given host (Juarez Heredia et al. 2014; Castillo et al. 2018). More specifically, reports of endoparasites and ectoparasites found on species of Patagonian lizards do exist (Table 11.2, Fig. 11.4g, h). In a recent review of reptile parasites in Chile, San Martín-Órdenes et al. (2019) report that *Liolaemus tenuis* is the species with the most diverse taxa of parasites registered (11 taxa and only three at species level) and that *Liolaemus chillanensis* has the highest number of identified species of parasites. Ecological or biological aspects resulting from the parasitic interaction have not been evaluated, as has been done for some non-Patagonian species.

For example, *Phymaturus extrilidus*, a species endemic to the Puna region, presents a greater intensity of nematodes in relation to a deficient body condition, greater environmental humidity, and to the monoxenic life cycle of the *Parapharyngodon riojensis* parasite (Castillo et al. 2018). As such, the average intensity of nematodes

Table 11.2 List of lizard species and parasites registered in the Patagonia region, Argentina, and Chile

Host lizard	Parasites	References
Salvator rufescens	*Styphlodora condita*	Lunaschi and Drago (2007)
Pristidactylus torquatus	*Eutrombicula araucanensis*	Stekol'nikov and González-Acuña (2015)
Leiosaurus belli	*Physaloptera retusa*	Goldberg et al. (2004)
Liolaemus austromendocinus	*Pterygosoma patagonica*	Dittmar De la Cruz et al. (2004)
Liolaemus bibroni	*Pterygosoma patagonica*	Dittmar De la Cruz et al. (2004)
Liolaemus boulengeri	*Parapharyngodon riojensis*	O'Grady and Dearing (2006)
Liolaemus buergeri	*Parapharyngodon riojensis*	Dittmar De la Cruz et al. (2004) and Goldberg et al. (2004)
	Pterygosoma patagonica	
Liolaemus chiliensis	*Spauligodon maytacapaci*	Goldberg et al. (2004) and San Martín-Órdenes et al. (2019)
	Pterygosoma sp.	
Liolaemus chillanensis	*Eutrombicula chillanensis*	Stekol'nikov and González-Acuña (2010, 2012, 2015) and Venzal et al. (2008)
	Eutrombicula liolaemi	
	Microtrombicula mapuche	
	Morelacarus sp.	
	Ornithodoros rioplatensis	
	Parasecia molini	
	Paratrombicula chilensis	
	Paratrombicula goffi	
Liolaemus curicensis	*Morelacarus* sp.	Stekol'nikov and González-Acuña (2015)
Liolaemus cyanogaster	*Pterygosoma cyanogasteri*	Fajfer and González-Acuña (2013)
Liolaemus elongatus	*Spauligodon maytacapaci*	Dittmar De la Cruz et al. (2004) and Goldberg et al. (2004)
	Pterygosoma patagonica	
Liolaemus gracilis	*Pterygosoma patagonica*	Dittmar De la Cruz et al. (2004)

(continued)

Table 11.2 (continued)

Host lizard	Parasites	References
Liolaemus lemniscatus	*Eutrombicula araucanensis*	Goldberg et al. (2004) and Stekol'nikov and González-Acuña (2012, 2015)
	Morelacarus sp.	
	Paratrombicula goffi	
	Spauligodon maytacapaci	
	Kiricephalus sp. *(nymphs)*	
Liolaemus monticola	*Eutrombicula paula*	Stekol'nikov and González-Acuña (2010, 2015)
Liolaemus neuquensis	*Physaloptera retusa*	Goldberg et al. (2004)
Liolaemus nitidus	*Diaguitacarus choapensis*	Muñoz Leal (2013), Fajfer (2015) and Stekol'nikov and González-Acuña (2015)
	Eutrombicula nerudai	
	Geckobia nitidus	
	Morelacarus sp.	
	Pterygosoma sp.	
Liolaemus petrophilus	*Pterygosoma patagonica*	Dittmar De la Cruz et al. (2004)
Liolaemus pictus	*Eimeria liolaemi*	Daszak and Ball (1998), Espinoza-Carniglia et al. (2016), Fajfer and González-Acuña (2013), Goldberg et al. (2004) and Stekol'nikov and González-Acuña (2010)
	Eutrombicula araucanensis	
	Pterygosoma sp.	
	Pterygosoma formosus	
	Pterygosoma levissima	
	Pterygosoma ligare	
	Pterygosoma ovata	
	Spauligodon maytacapaci	
Liolaemus rothi	*Parapharyngodon riojensis*	O'Grady and Dearing (2006)
Liolaemus septentrionalis	*Eutrombicula araucanensis*	Stekol'nikov and González-Acuña (2010, 2015) and Espinoza-Carniglia et al. (2015, 2016)
	Microtrombicula sp.	
	Morelacarus sp.	
	Parasecia sp.	
Liolaemus schroederi	*Morelacarus* sp.	Stekol'nikov and González-Acuña (2015)

(continued)

Table 11.2 (continued)

Host lizard	Parasites	References
Liolaemus tenuis	*Eutrombicula alfreddugesi*	Contreras et al. (1990), Daszak and Ball (1998), Goldberg et al. (2004), Rubio and Simonetti (2009) and Stekol'nikov and González-Acuña (2015)
	Eutrombicula araucanensis	
	Eimeria liolaemi	
	Morelacarus sp.	
	Pharyngodon sp.	
	Pterygosma sp.	
	Spauligodon maytacapaci	
	Veversia sp.	
Phymaturus damasense	*Parasecia molini*	Stekol'nikov and González-Acuña (2015)
Phymaturus tenebrosus	*Ornithodoros* sp.	Cabezas-Cartes et al. (2018b)
Phymaturus vociferator	*Eutrombicula chillanensis*	Venzal et al. (2008) and Marchant (2010)
	Eutrombicula liolaemi	
	Ornithodoros rioplatensis	
Phymaturus zapalensis	*Parapharyngodon riojensis*	O'Grady and Dearing (2006)

would be a good estimate to detect deficient physiological conditions of hosts (Castillo et al. 2018). Juarez Heredia et al. (2014) report ectoparasitic interaction between *Liolaemus pacha*, a species of lizard from northern Argentina which inhabits the Monte and Prepuna regions, and a mite of the genus *Pterygosoma.* These authors do not find seasonal variations with respect to mite intensity but do observe variation between sexes, with males having greater infestations than females. *Liolaemus pacha* males could be more exposed to ectoparasites as they have a greater "home range" than females (Halloy and Robles 2002), and on the other hand, hormonal imbalances of males during the reproductive season are generally associated with immune suppression, and as such, males are more susceptible to diseases or parasitosis (Salvador et al. 1996; Juarez Heredia et al. 2014). Carothers and Jaksić (2001) compared the distribution of ten *Liolaemus* species with the distribution of nematodes, ticks, mites, and the *Plasmodium* parasite with the objective of verifying if parasitism could be a determining factor for the limits of distribution of these lizards in the central Andes of Chile. These authors suggest that other interactions such as competition, predation, or environmental characteristics have a more predominant role in the altitudinal distribution of *Liolaemus* lizards, as opposed to parasitism. Jiménez (2005) compared the composition and magnitude of helminth parasites of three host populations of *Liolaemus tenuis* in Chile in order to assess whether the degree of environmental intervention is a determining factor in parasitic communities. Results indicated that there were differences in composition and parasitic magnitude, which could be due to differences in the composition of the lizard assemblage, the population density of *L. tenuis,* and the history of colonization in the different sites (regions with few individuals would present a smaller pool of parasites and loss of intermediate hosts; Garín and González-Acuña 2008).

Detailed studies relating the intensity and prevalence of parasites on lizards with biological and environmental variables have not been carried out in the Patagonia region. For this reason, it is necessary to conduct studies that contribute to our understanding of the function that parasitism has as an important component of the region's ecological systems.

11.5 Resource Partitioning

A recurring question in ecological studies is why an assemblage of species exists in a certain area or how species with similar requirements interact and persist (Vitt and Caldwell 2013). One of the main answers to these questions is that available resources are limited and therefore an assemblage of species must divide these resources in order to survive. Consequently, lizard interactions such as competition, predation, and parasitism, among others, are mechanisms that determine which species will persist and which will not, at least for local assemblages (Pianka and Huey 1978; Vitt and Caldwell 2013). An assumption in ecology is that an assemblage's structure is strongly determined by interspecies competition, as resources such as food and space are limited (Pough et al. 2001). Competition for limited resources could determine how many species are able to coexist, what features they possess, and what different uses they make of these resources, under the assumption that segregation is what allows for coexistence (MacArthur 1972; Cody et al. 1975; Pough et al. 2001).

Resource partitioning between species within an assemblage is a mechanism that generally occurs in one or more principal niche aspects: space (microhabitat), activity time, and food, which is known as a complementary niche aspect (Schoener 1974; Pianka 1986). Moreover, competition and predation are not the only mechanisms which can lead to resource division, as other factors exist which operate independently of interspecific interactions, such as physiology, thermoregulation behavior, and morphological restrictions (Williams 1983; Pough et al. 2001), which could favor coexistence between sympatric species.

The diverse environments in Patagonia are home to numerous lizard assemblages, and it is likely that the coexistence of a highly diverse group of species is made possible, thanks to the partitioning of environmental resources. However, there are few integral studies of species' niche in the region that include temporal, spatial, and trophic interactions. Núñez (1996), for example, evaluated the use of time, space, and diet in the sympatric species *Liolaemus curis* and *L. curicensis* in Termas del Flaco, central Chile, in order to infer which factors intervene in their coexistence. Both species are saxicolous, but they occupy rocks of different sizes and heights to sunbathe, which means they are not syntopic as they divide their microhabitat preferences. Nonetheless, spatial resource partitioning is not a competition mechanism but rather is due to intrinsic factors like body size and feeding, with a clear relationship existing between type of shelter and trophic offering provided by bushes. In terms of the temporal aspect, *L. curis* is bimodal while *L. curicensis* displays a unimodal pattern (active mainly in the morning). In this case, temporal segregation is determined by predator pressure and by different thermal requirements and behaviors of each species. The division of the thermal resource, determined by size and body mass, leads to a decrease in competitive interactions in other niche aspects, such as time and space (Barbault 1991; Pianka and Huey 1978; Gómez Alés et al. 2017b; Duran et al. 2018). Lastly, *L. curis* is an anteater while *L. curicensis* is a generalist in its feeding preferences. These differences are associated with the nutritional offering at the lizards' perch sites. As such, microhabitat use is the principal niche aspect allowing these species to coexist (Núñez 1996). On the other hand, Núñez et al. (1989) evaluated the degree of overlap between two syntopic species, *Liolaemus lemniscatus* and *L. fuscus*, in central Chile, considering three fundamental axes of the ecological niche (microhabitat, time, and food use) and incorporating seasonal variations. These authors found great similarities in the three dimensions of the niche during all seasons; the greatest overlap of microhabitat and time occurs during the seasons of abundant trophic resources (spring, summer), while during periods of food shortages (fall, winter) the overlap in diet and use of time is smaller (Núñez et al. 1989).

Conveying the importance of competition generally requires experimental manipulations in the field in order to be able to evaluate at a single site the use that a species in sympatry with another makes of resources in the absence of competition (Núñez et al. 1989). Nevertheless, though these situations are not frequent, they do occur naturally. In the Payunia region of southern Mendoza, Argentina, two *Phymaturus* species coexist in sympatry on volcanic rock. *Phymaturus roigorum* and *P. payuniae* are herbivorous, viviparous lizards that can often be observed sunbathing on the same rocks and sharing shelters (Corbalán and Debandi 2013). Specifically, *P. roigorum* is found to be both in allopatry and syntopy with *P. payuniae*, which represents an excellent natural scenario for evaluating the effect of competition on resource partitioning. Corbalán and Debandi (2014) demonstrated that for these strictly herbivorous species, diet segregation is the niche aspect that best explains their coexistence. Their foraging times are different (unimodal for *P. payuniae* and bimodal for *P. roigorum*) at one of the sites where they are found in syntopy and where diet overlap is high. On the other hand, this study does not provide sufficient evidence to be able to conclude that competition among species is present in this system. *P. roigorum's* activity and behavior patterns were not different at syntopy and allopatry sites, indicating that the presence of *P. payuniae* has no influence (Corbalán and Debandi 2014). These authors present the hypothesis of habitat quality to explain the presence of larger *P. roigorum* males at syntopy sites and the absence of *P. payuniae* at allopatric sites, due to the fact that sympatric sites have a greater proportion of adequate thermal microsites and food that these lizards prefer, such as *Fabiana punensis* and *Ephedra chilensis*, both absent at the allopatric sites.

Finally, intrinsic factors of life history such as body size, sex, or reproductive condition can help to minimize niche overlap in sympatry (Pianka 1973, 1986; Pough 1973; Vitt 2000; Pough et al. 2001), as has been observed, for example, in *Salvator rufescens*. This red iguana is widely distributed in the phytogeographical regions of the Monte and Chaco near the Patagonia region. In one of the Chaco sectors, this species is found to be in sympatry with *Salvator merianae,* and it has also been observed that body size, sexual maturity, and reproductive activity are relevant factors that influence diet (López Juri et al. 2015). As such, this is an example of how life history characteristics for these species influence diet composition and contribute to the coexistence of species by means of interspecific segregation of the trophic niche (López Juri et al. 2015). On the other hand, Cardozo et al. (2012) observed that these *Salvator* species differ in terms of habitat requirements when found in allopatry, while in the distribution contact zone they utilize the same habitat resources. Nevertheless, *S. rufescens* is associated with greater forest coverage, which could be determined by a trophic preference for native fruits and seeds (Cardozo et al. 2012).

11.6 Conclusions

There is abundant evidence to suggest that reptiles have entered into a process of biological diversity loss on a global scale due to human actions like habitat fragmentation and disturbances such as overgrazing, deforestation, forest clearing, expansion of agricultural borders, and global climate change (Acosta et al. 2018). Therefore, it is essential to deepen our knowledge of the diversity and ecology of this group as a fundamental step for its protection, conservation, and management. Throughout this chapter, we have been able to gather valuable information about Patagonian lizards regarding behavioral aspects and the use of trophic, temporal, and spatial resources, as well as its key role in the diverse Patagonian ecosystems (interspecific interactions). However, there are some challenges in filling information gaps that we have presented in each section. For example, knowledge about the role that parasitism can play in behavior, activity patterns, thermoregulation, and the survival of an organism is currently poor, although it should be included in any comprehensive strategy for reptile conservation.

To conclude, in a context of conservation of the diversity of Patagonian lizards and their environments, it is necessary to be aware of diverse biological and ecological parameters. In this sense, the analysis of the abundance of species is of utmost importance and is essential to evaluating seasonal and annual variations in different populations. There are few studies that seek to measure the population density of Patagonian lizards. This negatively affects conservation measures needed in the face of ever-increasing human activity, which compromises both environments and their species. Although this is a daunting task, we challenge researchers to continue publishing on diverse aspects of lizard ecology with special emphasis on long-term studies that evaluate the population dynamics of the species.

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Chapter 12

Reproductive Biology of Lizards from Patagonia, Argentina: Physiological and Behavioral Adaptations to Cold and Harsh Environments

Jorgelina M. Boretto, Jimena B. Fernández, Facundo Cabezas-Cartes, Marlin S. Medina, and Nora R. Ibargüengoytía

Abstract In this chapter, we provide a detailed and integrated review of the reproductive biology and life-history traits related to reproduction of lizards that inhabit the cold and harsh environments of Patagonia, Argentina. Lizards of the genera *Liolaemus*, *Phymaturus,* and *Homonota* have shown distinctive life-history traits, such as the retention of eggs in the oviducts during most of embryogenesis, evolutionary transitions from oviparity to viviparity, adaptive synchronization of parturition under benign environmental conditions, signs of parental care, plasticity in the timing of reproductive events, prolonged multiennial reproductive cycles in females, interspecific variability in male reproductive cycles, and physiological mechanisms in males to synchronize with female cycles, among others. We discuss the adaptation of reproductive cycles to the energetic constraints imposed by environmental conditions of Patagonia. We focus on understanding how reproductive physiology could be affected by environmental stressors with the aim of contributing to successful conservation strategies.

J. M. Boretto (✉)
Instituto de Investigaciones en Biodiversidad y Medioambiente, Consejo Nacional de Investigaciones Científicas y Técnicas (INIBIOMA, CONICET-Universidad Nacional del Comahue), San Carlos de Bariloche, Río Negro, Argentina
e-mail: borettojm@comahue-conicet.gob.ar

J. B. Fernández · F. Cabezas-Cartes · N. R. Ibargüengoytía
Instituto de Investigaciones en Biodiversidad y Medioambiente, Consejo Nacional de Investigaciones Científicas y Técnicas (INIBIOMA-CONICET), San Carlos de Bariloche, Río Negro, Argentina
e-mail: jimenafernandez@comahue-conicet.gob.ar; norai@comahue-conicet.gob.ar

M. S. Medina
Centro de Investigación Esquel de Montaña y Estepa Patagónica, Consejo Nacional de Investigaciones Científicas y Técnicas (CIEMEP-CONICET), Universidad Nacional de la Patagonia San Juan Bosco, Esquel, Chubut, Argentina

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12.1 General Introduction

Animal conservation concerns the understanding of the physiological responses of organisms to environmental changes. Thus, the study of life-history traits, including reproductive mode (Tinkle and Gibbons 1977), rate of reproduction, age at maturity and longevity (Tinkle et al. 1970; Dunham et al. 1988; Stearns 2000; Gotthard 2001), relative timing of each reproductive event including births or hatchings (Tinkle and Gibbons 1977; Saint Girons 1985; Pough et al. 1998), and endocrine control (Ricklefs and Wikelski 2002), provides the knowledge to lay the groundwork for conservation strategies to be successful. In Patagonia, Argentina, lizards must cope with climatic and thermal restrictions, since the cold-temperate climate imposes a strong seasonal cycle of resource and energy availability. Unlike tropical lizards that usually reproduce at least once per year, cold-temperate lizards are distinctly seasonal, alternating periods of reproduction and brumation (winter inactivity in ectothermic vertebrates; Mayhew 1965; Duvall et al. 1982; Guillette and Casas-Andreu 1987) and in more extreme conditions cycles are multiennial (prolonged). These limitations depend not only on temperature, but also on food availability, the opportunity to store energy in fat bodies that females later mobilize for vitellogenesis (Saint Girons 1985; Van Wyk 1991; Pough et al. 1998), and internal factors like the endocrine control (Duvall et al. 1982; Callard et al. 1992; Custodia-Lora and Callard 2002; Boretto et al. 2010a). Long summer droughts, and cold, snowy winters, typical of arid zones of Patagonia (Cabrera 1976; Paruelo et al. 1998), result in particular patterns of thermoregulatory behavior (Ibargüengoytía 2005; Medina et al. 2009; Ibargüengoytía et al. 2008, 2010; Duran et al. 2018), growth (Piantoni et al. 2006a, b; Gutiérrez et al. 2013; Boretto et al. 2018; Cabezas-Cartes et al. 2015, 2018a) and reproductive traits. Thus, lizard species that inhabit Patagonia are an appealing model for the study of life-history adaptations to cold and harsh environments, where a large proportion of the year is unsuitable for growth and reproduction. The study of their life histories provides valuable background for the analysis of physiological responses to changing environments and for the understanding of how physiology, reproduction, phenology, population dynamics, life cycles, and demography are affected by environmental stressors including not only chronic disturbances such as global climate change but also acute stressors like fires, volcanic eruptions, and anthropogenic activities.

In the present chapter, we review and integrate current knowledge of reproductive biology in a broad sense. We discuss the studies of oviparous and viviparous lizards in Patagonia, including those on male and female reproductive cycles, parental care, life-history parameters obtained by skeletochronology, and hormonal control of reproduction. Some of these studies were overriding when we were studying the disruptive effects of an environmental stressor, the eruption of the Puyehue-Cordón Caulle volcano complex, on reproduction and body condition of *Phymaturus* *spectabilis* (=*Phymaturus spurcus* Barbour 1921 sensu Becker et al. 2019; Boretto et al. 2014a), underscoring the relevance of basic knowledge to understand the physiological responses of organisms to their dynamic environment.

At high altitudes and latitudes, adaptive adjustments in the timing of reproductive events such as gametogenesis, embryonic development, and hatching or birth become of vital importance to optimize performance within the short and dry activity seasons characteristic of most of Patagonia. Lizards of the genera *Liolaemus*, *Phymaturus,* and *Homonota* show distinctive life-history traits, such as the retention of eggs in the oviducts during most of embryogenesis, evolutionary transitions from oviparity to viviparity, adaptive synchronization of parturition with benign environmental conditions, signs of parental care, plasticity in the relative time of reproductive events, prolonged reproductive cycles in females, particular hormonal control of male and female reproduction, and interspecific variability in the male reproductive cycles, among others. In each section of this chapter, we will discuss how lizard species adjust their reproductive cycles according to the energetic restrictions imposed by the environmental conditions of Patagonia, with the view that bioenergetics is their fundamental constraint on their ability to cope with environmental stressors, and that stress, represents any change in the environment that causes an organism to allocate energy away from reproduction to another function.

12.2 Reproductive Cycles of Oviparous Females

Successful reproduction in ectotherms requires an adaptation of physiology to environmental factors like temperature, precipitation, photoperiod, seasonality, and length of the activity season, among others (Saint Girons 1985). Under the cold and harsh Patagonian climate, reproduction and growth of lizards are restricted to brief seasons, particularly at high latitudes (Ibargüengoytía 2004; Piantoni et al. 2006a, b; Medina and Ibargüengoytía 2010). The environmental conditions of Patagonia are characterized by strong climatic seasonality, with dry summers, frost at any time of year, and snow in winter (Cabrera 1976; Chap. 4). Spring and autumn provide only short transitions between summer and winter (Paruelo et al. 1998). These environmental conditions result in distinctive features in thermal biology (Ibargüengoytía 2005; Medina et al. 2009; Ibargüengoytía et al. 2008) and reproductive traits in lizards. Particularly in oviparous species inhabiting high latitudes, the adaptive adjustments in the timing of the reproductive events, such as gametogenesis, embryonic development, nesting, and hatching, are vitally important to success within the short and dry activity season. Environmental conditions are expected to more strongly constrain oviparous species firstly because of the effect of high variation in daily and seasonal temperatures on body temperature, and secondly because cold temperatures and dehydration are detrimental to the rate of embryonic developmental and subsequent offspring fitness (Packard et al. 1977; Qualls and Andrews 1999). Oviparous species usually are adapted to cold climates by laying their eggs in early summer (Shine 1985), allowing hatchlings to feed, grow, and store sufficient energy prior to the onset of brumation (Olsson and Shine 1997).

Studies on life history of lizards from Patagonia confirm the presence of oviparity in numerous species from the genera *Liolaemus*, *Diplolaemus*, *Leiosaurus*, *Pristidactylus*, *Teius,* and *Homonota* (reviewed by Cei 1986; Ibargüengoytía 2004; Scolaro 2005) and document data, for example, about clutch size (e.g., in *Leiosaurus bellii*; Avila and D'Hervé 1999; and see Cei 1986 for numerous species). Nevertheless, the reproductive biology has been completely studied in only two species of *Liolaemus* and one species of *Homonota*. *Liolaemus bibronii* and *Liolaemus boulengeri* were studied in two sites at different latitudes in Patagonian steppe (43° S and 46° S) to infer how spatial variation in environmental factors affects the timing of reproductive cycles of oviparous species (Medina and Ibargüengoytía 2010). These species are syntopic, have a similar body size, and are insectivorous (Cei 1986). Both species experience seasonal variations in environmental temperatures, long periods of brumation during autumn and winter, and an activity period of approximately 6–7 months (Medina et al. 2011). Populations of both oviparous species at low and high latitude show annual and synchronous reproductive cycles between males and females (Table 12.1). Females start vitellogenesis in early summer, immediately after oviposition, but it is arrested or very slow during brumation and rapidly resumes in spring when ovulation and copulation occur (Medina and Ibargüengoytía 2010; Table 12.2). In addition, ovigerous females are found until the end of spring, indicating that oviposition occurs from late spring to early summer (Medina and Ibargüengoytía 2010; Table 12.2), ensuring that the colder temperatures occur at the end of the developmental period, when it is expected to have relatively little effect on hatching date (Shine 2002). Hatch occurs in midsummer after approximately 2–3 months of incubation. Even in the southern populations, where there are significantly lower microenvironmental temperatures for thermoregulation (Medina et al. 2009), females of *L. bibronii* and *L. boulengeri* seem to be able to use nest sites sufficiently warm for embryogenesis to be completed within the short summer season (Medina and Ibargüengoytía 2010).

In contrast, females of the southernmost gekkonid *Homonota darwinii* skip a year of reproduction, developing an annual-biennial cycle (Ibargüengoytía and Casalins 2007; Table 12.1). *Homonota darwinii* is a saxicolous small gecko, entirely oviparous, with crepuscular or nocturnal habits, and a wide distribution (35°–52° S and 63°–73° W; Cei 1986, 1993). The female gonadotrophic analyses showed that right and left follicles grow similarly to approximately 3 mm diameter, and then vitellogenesis stops in one follicle and continues in the other (allochrony; Ibargüengoytía and Casalins 2007). Vitellogenesis lasts about 1 year, since it begins in spring and continues through autumn, but it is arrested or very slow during winter brumation, until the spring of the next year, when it rapidly resumes and ovulation takes place (Table 12.2). Females captured in spring possessed either one egg in utero or none at all. Simultaneously, some females showed only small vitellogenic follicles (<3 mm), lasting until late summer, and only medium-sized follicles were seen in autumn. This evidence suggests that females reproduce annually or biennially and that a reproductive cycle may or may not be followed by another (skip a year of reproduction; Ibargüengoytía and Casalins 2007). The production of only one offspring per reproductive annual-biennial cycle results in a mean annual reproductive output of 0.75, one of the lowest values reported for lizards (Cree 1994;

Table 12.1 Characteristics of the reproductive cycles of lizards from Patagonia, Argentina (from 39° S, 70° W, 500–1800 m a.s.l. to 51° S, 71° W, 133 m a.s.l.)

Species	Locality (latitude, longitude, and altitude)	Mode of reproduction	Female frequency of reproduction	Litter/ clutch size	Mean annual reproductive output	Male reproductive cycle	Sperm storage
Liolaemus elongatus[a,b]	39–41° S, 70.5–71.6° W, 500–1800 m a.s.l.	Viviparous	Annual-biennial	3–7	3.75	Seasonal	No
Phymaturus zapalensis[c]	39.73° S, 70.37° W 824–1312 m a.s.l.	Viviparous	Annual-biennial	1–2	1.12	Postnuptial	No
Phymaturus spectabilis (= *P. spurcus*)[d,e]	41° S, 69° W, 983–1064 m a.s.l.	Viviparous	Annual-biennial	1–3	1.5	Postnuptial	No
Phymaturus tenebrosus[f]	40.5–41.6° S, 70.5–71.5° W, 575–1230 m a.s.l.	Viviparous	Biennial	2	1	Postnuptial	Yes
Liolaemus pictus[g]	41.17° S, 71.42° W, 711 m a.s.l.	Viviparous	Biennial-triennial	3–6	1.9	Continuous	Yes
Homonota darwinii[h]	41–45° S, 69–71° W, 800 m a.s.l.	Oviparous	Annual-biennial	1	0.75	Postnuptial	Yes
Liolaemus bibronii[i]	43° S, 70° W, 626 m a.s.l. and 46° S, 71° W, 263 m a.s.l.	Oviparous	Annual	2–4	3	Postnuptial	Yes
Liolaemus boulengeri[i]	43° S, 70° W, 626 m a.s.l. and 46° S, 71° W, 263 m a.s.l.	Oviparous	Annual	2–5	3.5	Postnuptial	Yes
Liolaemus lineomaculatus[i]	43° S, 70° W, 626 m a.s.l. and 46° S, 71° W, 263 m a.s.l.	Viviparous	Annual	2–4	3	Postnuptial	Yes
Liolaemus sarmientoi[j,k]	50° S, 72° W, 80 m a.s.l. and 51° S, 71° W, 133 m a.s.l.	Viviparous	Annual-biennial	2–7	3.09	Continuous	Yes
Liolaemus magellanicus[j,k]	51° S, 71° W, 133 m a.s.l.	Viviparous	Annual-biennial	3–4	2.55	Continuous	Yes

[a] Ibargüengoytía and Cussac (1998); [b] Ibargüengoytía and Cussac (1999); [c] Boretto and Ibargüengoytía (2009); [d] Boretto et al. (2014a, b); [e] Cabezas-Cartes et al. (2015); [f] Ibargüengoytía (2004); [g] Ibargüengoytía and Cussac (1996); [h] Ibargüengoytía and Casalins (2007); [i] Medina and Ibargüengoytía (2010); [j] Fernández et al. (2015); [k] Fernández et al. (2017)

Dunham et al. 1988; Boretto et al. 2007; Cabezas-Cartes et al. 2010; Table 12.1). The reproductive female cycle described for *H. darwinii* in Patagonian environments is more similar to that of reptiles from temperate environments of the Southern Hemisphere than with other *Homonota* species from Argentina (Ibargüengoytía and Casalins 2007).

The studies of female reproductive cycles of oviparous lizard species of Patagonia revealed different strategies to cope with the temporal and spatial variation in environmental factors, which results in differences within and among species in the timing of reproductive cycles. The syntopic oviparous liolaemids *Liolaemus bibronii* and *L. boulengeri* show the capacity to appropriately allocate energy to the functions of maintenance, storage, growth, and reproduction, optimizing investment into reproduction to attain a steady annual cycle. In contrast, the female reproductive cycle of *Homonota darwinii* appears to be strongly affected by the shorter activity season that limits thermal and feeding opportunities, resulting in the inability to reproduce each year.

12.3 Reproductive Cycles of Viviparous Females

Individual and adaptive responses to different environments are limited by physiological mechanisms. Although energy and material allocations are important results of physiological trade-offs, endocrine control mechanisms can produce incompatible physiological states that restrict life histories to a single dominant axis of variation (Ricklefs and Wikelski 2002). In this sense, in viviparous female lizards, high levels of progesterone during gestation inhibits follicular development and vitellogenesis, limiting the reproductive cycle due to the physiological inability of females to perform vitellogenesis while gravid (Duvall et al. 1982; Callard et al. 1992; Custodia-Lora and Callard 2002). Though studies of endocrinology in liolaemid lizards are incomplete, a preliminary study in some species of the viviparous genus *Phymaturus* showed high levels of progesterone and low or non-detectable levels of estrogen in pregnant females of *Phymaturus antofagastensis* and *Phymaturus aguanegra* endemic to cold environments at high altitudes in the Andes Mountains (Boretto et al. 2010a). Similarly, females of *Phymaturus zapalensis*, endemic to the National Park Laguna Blanca and its surroundings in Patagonia (39° S and 70° W, 800–1300 m a.s.l.), exhibited higher levels of progesterone during early and medium gestation stages than during late pregnancy or during the vitellogenic period (Boretto et al. 2010a). These preliminary results suggest that the endocrine control mechanism produces incompatible physiological states in at least some liolaemids, which, together with the thermal and energetic constraints of cold environments, restricts life histories, and particularly the reproductive cycles, toward a dominant axis: the prolonged female reproductive cycle.

There are different conditions in a female reproductive cycle that may drive to a prolonged multiennial cycle: (1) a prolonged vitellogenesis (van Wyk 1991; Cree and Guillette 1995; Cree et al. 1992; Ibargüengoytía 2004; Boretto and Ibargüengoytía 2006), (2) prolonged pregnancy (Vial and Stewart 1985; Cree and Guillette 1995;

Habit and Ortiz 1996; Olsson and Shine 1999; Wilson and Cree 2003), (3) allocation of vitellogenesis and pregnancy in separate breeding seasons (Ibargüengoytía and Cussac 1996; 1998; Boretto and Ibargüengoytía 2006; Boretto et al. 2007; Cabezas-Cartes et al. 2010), and (4) skipping of a year (van Wyk 1991; Ibargüengoytía and Cussac 1996; Boretto and Ibargüengoytía 2009). In consequence, one of the established detection criteria of biennial reproductive cycle (one litter every 2 years) is the co-occurrence of vitellogenic and pregnant females (discarding an effect of snout-vent length; Cree and Guillette 1995; Ibargüengoytía and Cussac 1996; Boretto et al. 2014b). Another criterion to determine the existence of biennial cycles is that half of adult females are nonreproductive during the breeding season, without temporal overlap of vitellogenesis and pregnancy (Aldridge 1979; van Wyk 1991; Ibargüengoytía and Casalins 2007; Boretto and Ibargüengoytía 2009). In this last case, females skip a year before starting the next vitellogenic cycle (van Wyk 1991).

Multiennial prolonged female reproductive cycles in Patagonia, Argentina, were first described in *Liolaemus pictus* (41° 07′ S, 71° 20′ W, 771 m a.s.l.; Ibargüengoytía and Cussac 1996; Tables 12.1 and 12.2). The cycle is biennial to triennial and females produce one litter every 2 or even 3 years, due to prolonged vitellogenesis that begins in late spring and continues through the summer and early autumn, being completed after a period of latency or low follicle growth over winter (Ibargüengoytía and Cussac 1996). After brumation, ovulation and mating occurs the next spring, and gestation extends from late spring to summer when parturition takes place during late summer or early autumn (Ibargüengoytía and Cussac 1996). During spring, as some females ovulate and mate, others start a new vitellogenic cycle, and still others (approximately 20%) remain nonreproductive until summer and early autumn, evidence of a biennial to triennial pattern, due to the skipping of a year (Ibargüengoytía and Cussac 1996). Similarly, in *Phymaturus zapalensis* from northern Patagonia, in Neuquén Province, about half of females skip a reproductive year as evidenced by the presence of only small oocytes (Boretto and Ibargüengoytía 2009). At the same time, the other females reproduce annually, performing vitellogenesis in spring and proceeding through pregnancy from late spring to midsummer (Boretto and Ibargüengoytía 2009; Table 12.2). The attainment of an annual cycle by half of females is probably permitted by the ability of postpartum females to acquire and store energy in autumn, as a necessary prerequisite for the onset and progress of vitellogenesis into the following year. Such energy availability stems from the fact that this species lives in a more-temperate climate, with longer activity seasons, than *L. pictus* or their biennial Patagonian congeners like *Phymaturus tenebrosus* (Ibargüengoytía 2004).

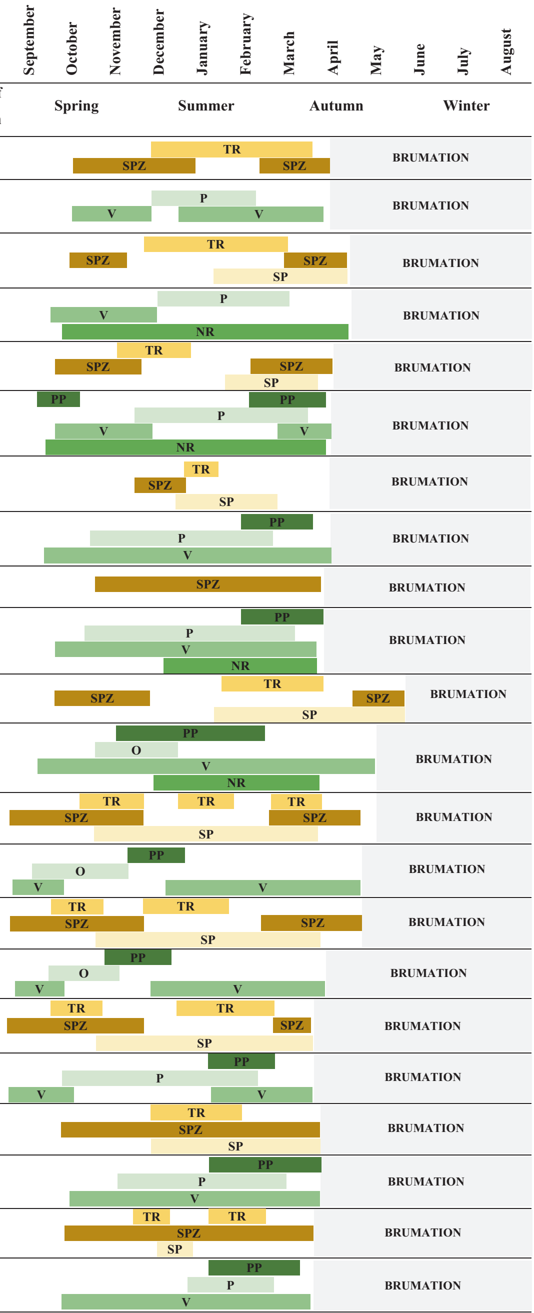
Likewise, females of *Phymaturus spectabilis* (= *P. spurcus*) from Ingeniero Jacobacci in Río Negro Province (41° S, 69° W, 1000 m a.s.l.) can display an annual cycle in which vitellogenesis begins in early autumn and finishes in midspring, and pregnancy occurs from late spring to midsummer (Boretto et al. 2014b; Table 12.2). Nevertheless, half of adult females were observed in a nonreproductive condition during the entire reproductive season, although the others were vitellogenic or gravid, evidencing a biennial cycle due to the skipping of a year of reproduction (Boretto et al. 2014b; Table 12.2). Boretto et al. (2014b) were the first in Argentina to use a noninvasive method of abdominal palpation to determine the female reproductive cycle, a critical tool in the study of low-viability populations such as those within the genus *Phymaturus* (Abdala et al. 2012).

Annual-biennial female cycle was described in *Liolaemus elongatus* from populations of the Patagonian steppe in Río Negro Province (40° S 71° W, 500–1800 m a.s.l.; Ibargüengoytía and Cussac 1998) and in the sympatric species *Liolaemus sarmientoi* and *L. magellanicus* in Santa Cruz Province (50° S 72° W, 80 m a.s.l., and 51° S, 69° W, 109 m a.s.l.; Fernández et al. 2015; Table 12.2). Adult females of *L. elongatus* begin vitellogenesis in summer and is completed in spring when mating occurs. Pregnancy extends from spring to mid summer, completing the cycle in 1 year. Nevertheless, the simultaneous presence of females showing early pregnancy and early vitellogenesis in spring and the co-occurrence of adult females with small follicular sizes and females with large follicular sizes, indicate that about half of the females perform a biennial cycle (Ibargüengoytía and Cussac 1998; Table 12.2). This is also the case of the southernmost reptiles of the world, the sympatric species *L. sarmientoi* and *L. magellanicus* that reproduce annually or biennially. These lizards live in one of the harshest climates of Patagonia (50–51° S) and are active for only about 5 months from late spring to the end of summer, when vitellogenesis, mating, pregnancy, and birth take place. Vitellogenesis in both species starts in late spring, continues through summer, undergoes cessation in winter, and resumes to completion in early spring, a process of about 10 months. Vitellogenesis is followed by mating, and pregnancy occurs from late spring to midsummer and births in midsummer (Fernández et al. 2015). Females that give birth earlier in summer can start a new vitellogenic cycle before autumn and perform an annual reproductive cycle. The births in early summer allow offspring to maximize their growth before their first winter and, in both juveniles and females, to increase their lipid reserves during the rest of summer. However, those females that give birth later in summer delay the start of a new vitellogenic cycle until the next spring, performing a biennial reproductive cycle. Thus, *L. sarmientoi* and *L. magellanicus* females reproduce annually or biennially, probably depending on the intensity of energetic restrictions imposed by the cold-temperate, harsh, and fast-changing weather of austral South America (Fernández et al. 2015; Table 12.2). In contrast, the study of two populations of *L. lineomaculatus* at low and high latitudes (43° S and 46° S, Chubut and Santa Cruz Province) showed both annual reproductive cycles. Females of *L. lineomaculatus* start vitellogenesis in midsummer, and the process lasts 9 months until the next spring, when ovulation occurs. Pregnancy begins in spring and the co-occurrence in early summer of pregnant females with advanced embryonic developmental stages and postpartum females, and the observation of youngest juveniles in midsummer suggests that births occur during this period (Medina and Ibargüengoytía 2010). Plasticity in the timing and duration of female reproductive cycles probably allows lizards to inhabit a wide range of steppe and cold montane environments, as is the case of *L. elongatus* and *L. lineomaculatus*, or to cope with the short activity season in the cold and unpredictable environments of Patagonia, as observed in *P. zapalensis* and *P. spectabilis* (= *P. spurcus*) and with the sympatric species *L. sarmientoi* and *L. magellanicus*. In particular, when the activity seasons are short and cold and feeding opportunities are limited, females need to replenish their energetic resources the following season to grow and store energy for the next reproductive cycle, whereas under more benign environmental conditions, the female reproductive cycles of liolaemids can be resumed in a year, as seen in the study of *L. lineomaculatus* (Medina and Ibargüengoytía 2010).

Meanwhile, strictly biennial female reproduction was found in *Phymaturus tenebrosus*, in populations of Neuquén and Río Negro Provinces (41° S and 71° W), in which vitellogenesis and pregnancy occur in different years resulting in the simultaneous presence of vitellogenic and pregnant females during the entire activity season (Ibargüengoytía 2004; Table 12.2). The most prolonged process is vitellogenesis, lasting 1 year, whereas gestation lasts approximately 4 months starting in midspring. After parturition at the end of summer, females become reproductively quiescent for approximately 8 months from autumn until the next activity season, when vitellogenesis begins in spring (Ibargüengoytía 2004).

The reproductive biology of viviparous Patagonian lizards showed that cold environments, coupled with hormonal and physiological restrictions inherent to viviparity (Callard et al. 1992; Custodia-Lora and Callard 2002; Boretto et al. 2010a), often prevent females from completing vitellogenesis, pregnancy, and the replenishment of new fat stored within one activity season, resulting in prolonged multiennial cycles. Causal relationships between the timing of reproduction and the access to suitable thermal microenvironments are complex, since environmental temperature also exerts strong influence on food availability. In consequence, despite the differences in the timing of vitellogenesis and gestation among Patagonian liolaemids, births occur during mid to late summer in all of them (Table 12.2). The convergence in the timing of birth highlights the constraints imposed by Patagonian climate on the timings of reproduction of females and the availability of food and heat necessary for digestion, assimilation, and fat storage for females and newborns to enter in brumation. If parturition occurs under more benign environmental conditions, greater neonate survival is expected, especially in species with low litter sizes like those in *Phymaturus* (Table 12.2). In addition, in all species of the *Phymaturus patagonicus* group (Chaps. 7 and 9), as in all studied *Liolaemus*, females exhibit a larger inter-limb length than males (Boretto and Ibargüengoytía 2009; Boretto et al. 2014b; Medina and Ibargüengoytía 2010; Fernández et al. 2017), attributed to fecundity selection for increasing the space to hold the developing embryos (Andersson 1994; Olsson et al. 2002; Cox et al. 2003). Thereby, this sexual dimorphism could be the result of strong selection for greater embryo size, which could permit greater fat reserves in newborns as in *Phymaturus*, or could be an adaptation for greater litter size as in *Liolaemus* (Medina and Ibargüengoytía 2010; Fernández et al. 2017), a common pattern in species with small litter size (Olsson et al. 2002; Cox et al. 2003). Larger females that favor larger offspring are especially important in *Phymaturus*, since the low litter size (one to three) in addition to the prolonged annual-biennial or biennial female reproductive cycles results in a low mean annual reproductive output in all species (Table 12.1), these being among the lowest for reptiles worldwide (Cree 1994; Ibargüengoytía and Casalins 2007).

Table 12.2 Chronology of the reproductive cycles of Patagonian lizards. In males (♂) the spermatogenic stages are indicated as: spermatocytes and spermatids (SP), spermatozoa in testes and/or epididymis (SPZ), and testicular regression (TR). In females (♀) stages are indicated as: vitellogenic (V), ovigerous/pregnant females (O/P), post-partum females (PP), and non-reproductive females (NR)



Species	Sex	Frequency of reproduction	September October November December January February March April May June July August Spring Summer Autumn Winter
Liolaemus elongatus [a,b]	♂	Annual	TR SPZ SPZ BRUMATION
	♀	Annual–Biennial	P V V BRUMATION
Phymaturus zapalensis [c]	♂	Annual	TR SPZ SPZ SP BRUMATION
	♀	Annual–Biennial	P V NR BRUMATION
Phymaturus spectabilis (= *P. spurcus*) [d,e]	♂	Annual	TR SPZ SPZ SP BRUMATION
	♀	Annual–Biennial	PP PP P V V NR BRUMATION
Phymaturus tenebrosus [f]	♂	Annual	TR SPZ SP BRUMATION
	♀	Biennial	PP P V BRUMATION
Liolaemus pictus [g]	♂	Continuous	SPZ BRUMATION
	♀	Biennial–Triennial	PP P V NR BRUMATION
Homonota darwinii [h]	♂	Annual	TR SPZ SPZ SP BRUMATION
	♀	Annual–Biennial	PP O V NR BRUMATION
Liolaemus bibronii [i]	♂	Annual	TR TR TR SPZ SPZ SP BRUMATION
	♀	Annual	PP O V V BRUMATION
Liolaemus boulengeri [i]	♂	Annual	TR TR SPZ SPZ SP BRUMATION
	♀	Annual	PP O V V BRUMATION
Liolaemus lineomaculatus [i]	♂	Annual	TR TR SPZ SPZ SP BRUMATION
	♀	Annual	PP P V V BRUMATION
Liolaemus sarmientoi [j,k]	♂	Continuous	TR SPZ SP BRUMATION
	♀	Annual–Biennial	PP P V BRUMATION
Liolaemus magellanicus [j,k]	♂	Continuous	TR TR SPZ SP BRUMATION
	♀	Annual–Biennial	PP P V BRUMATION

[a] Ibargüengoytía and Cussac (1998); [b] Ibargüengoytía and Cussac (1999); [c] Boretto and Ibargüengoytía (2009); [d] Boretto et al. (2014a, b, c); [e] Cabezas-Cartes et al. (2015); [f] Ibargüengoytía (2004); [g] Ibargüengoytía and Cussac (1996); [h] Ibargüengoytía and Casalins (2007); [i] Medina and Ibargüengoytía (2010); [j] Fernández et al. (2015); [k] Fernández et al. (2017)

Recently, an experimental study in the European species *Zootoca vivipara* showed that warmer temperatures cause faster body growth, earlier maturation, and an increased voltinism, leading to a highly accelerated life cycle but also to a decrease in adult survival (Bestion et al. 2015). Experimental studies in lizards of Patagonia will be valuable to determine the impact of global warming on such life-history traits. Viviparous species with plastic female reproductive cycles (annual-biennial or biennial-triennial) could be expected to reproduce more frequently, increasing mean annual reproductive output. However, a faster life cycle would require higher feeding rates, and this is a constraint particularly in herbivorous species of *Phymaturus* in which females allocate a large proportion of energy into reproduction and where there is a selection of larger females to favor offspring size. In addition, females and males have to synchronize their reproductive cycles with each other. Although speculative, the most parsimonious hypothesis would be that if females can shorten reproductive cycles they would also have higher energetic demands, faster growth, and decreased longevity, like that observed in *Zootoca vivipara* (Bestion et al. 2015), affecting population viability.

12.4 Reproductive Cycles of Males

Male cycles depend largely on temperature, the timing of female cycles (Jones et al. 1997; Ibargüengoytía and Cussac 1999; Medina and Ibargüengoytía 2010), and the availability of receptive females (Leyton et al. 1982; Ibargüengoytía 2008; Méndez De la Cruz et al. 2014). In a first general instance, male reproductive cycles could be classified as seasonal or continuous. In populations where females have multiple clutches per year, such as in tropical and subtropical environments, most reptile males show a common pattern of continuous reproductive cycles, producing spermatozoa continuously probably as response to a predictable climate and a thermal constancy all year (Flemming 1994; Pough et al. 1998; Gribbins et al. 2009; Ortiz et al. 2014). In contrast, species with male seasonal cycles alternate periods of gonadal activity and spermatogenesis with periods of gonadal regression and quiescence (Crews and Gans 1992; Gribbins and Gist 2003; Méndez De la Cruz et al. 2014), which, in turn, can be synchronous or asynchronous with the female reproductive cycle. In synchronous cycles, spermatogenesis and vitellogenesis progress simultaneously until ovulation and mating, followed by testicular regression and a resting period. Synchrony between males and females is common in lizards from temperate and tropical climates that can assign long periods to reproduction (Crews and Gans 1992; Whittier and Tokarz 1992; Pudney 1995; Wu et al. 2015). In asynchronic cycles, male and female gametogenesis is not simultaneous, and sperm are stored in either or both females and males (Marion and Sexton 1971; Whittier and Tokarz 1992; Swain and Jones 1994; van Wyk 1995). Seasonal testicular cycles can be prenuptial or postnuptial, depending if the spermatogenic cycle occurs before or after mating (Moore and Lindzey 1992; Pudney 1995).

Lizards that inhabit harsh or extreme environments exhibit particular characteristics that allow them to successfully reproduce. Liolaemid males from cold-temperate climates have evolved a diversity of reproductive patterns to coordinate with the short female reproductive season and to deal with the low frequency of receptive females, as consequence of the prolonged female cycles (annual-biennial, biennial, or triennial cycles). Histological studies of testes and epididymis of liolaemids put in evidence that testicular size alone is a weak indicator of spermatogenic stage and sexual maturity (Ibargüengoytía and Cussac 1998; Ibargüengoytía 2004; Boretto and Ibargüengoytía 2006; Ibargüengoytía and Casalins 2007). Testicular size changes as consequence of the size of the interstitial space and the development of the seminiferous epithelium, which changes its cellular composition and functionality in relation to reproductive and endocrine activity. Studies in liolaemids have shown that testicular size does not correspond to spermatogenic stage or the development of luminal and interstitial tissue (Boretto and Ibargüengoytía 2006; Boretto et al. 2007; Fernández et al. 2017) and that spermiation does not always correlate with the largest testicular sizes (Leyton et al. 1977; Ibargüengoytía and Cussac 1998; Ibargüengoytía 2004). Based on histological studies, seasonal testicular cycles have been described in some species of Patagonia (Table 12.2). For example, the male reproductive cycle of *Homonota darwinii* is seasonal and highly synchronized among individuals. Males with spermatozoa in seminiferous tubules were found in autumn and spring, whereas testicular regression was observed in early and midsummer, and recrudescence occurred in mid to late summer, following an annual postnuptial pattern (Ibargüengoytía and Casalins 2007). The presence of spermatozoa in the epididymis of males with either spermatocytes or spermatozoa or displaying testicular regression strongly suggests that there is a reserve of spermatozoa during the entire activity season, from spring to autumn in *H. darwinii* (Ibargüengoytía and Casalins 2007; Table 12.2). Such sperm storage allows copulation at any time during the activity season and has been associated with brief activity seasons and dissociated cycles (Pough et al. 1998).

Likewise, postnuptial cycles have been described in *P. tenebrosus* (Ibargüengoytía 2004), *P. zapalensis* (Boretto and Ibargüengoytía 2009), and *P. spectabilis* (= *P. spurcus*; Boretto et al. 2014b). In *P. tenebrosus,* spermatogenesis begins in late spring and continues throughout summer until individuals enter brumation. After winter, the spermiogenesis resumes, and males are ready to copulate from mid to late spring with spermatozoa in the seminiferous tubules and the epididymis (Table 12.2). In this period, males showed highly developed Leydig cells in the interstitial tissue lying between seminiferous tubules, probably associated with a maximum concentration of testosterone characteristic of spermiogenesis and the mating season (Ibargüengoytía 2004), indicating that this postnuptial cycle is also an associated cycle. Nevertheless, spermatozoa are stored in the epididymis for 2 months until early summer in males with testicular regression, as well as in those males that are starting a new spermatogenic cycle, extending the time of availability of sperm to receptive females. Taking into account the period in which females have the greatest follicular sizes, males of *P. tenebrosus* reproduce in synchrony with females (Ibargüengoytía 2004).

Similarly, males of *P. zapalensis* and *P. spectabilis* (= *P. spurcus*) exhibited an annual reproductive cycle synchronous with the female cycle (Table 12.1). Males initiate the spermatogenic cycle in midsummer, and spermatids and spermatozoa testicular stages are present from early autumn to the next spring. In midspring, males show spermatozoa in epididymis, and females have enlarged follicles, indicating imminent ovulation (Boretto and Ibargüengoytía 2009; Boretto et al. 2014b; Table 12.2). The similarity among male reproductive cycles of *Phymaturus* that inhabit the Patagonian steppe of Argentina indicates a postnuptial pattern probably related to the annual-biennial female cycle among the *patagonicus* group (Chaps. 7 and 9), which differs from the strictly biennial female cycle observed in species of the *palluma* group (Habit and Ortiz 1996; Boretto and Ibargüengoytía 2006; Boretto et al. 2007; Cabezas-Cartes et al. 2010; Castro et al. 2018).

In contrast, in the genus *Liolaemus*, interspecific differences in male reproductive cycles are observed. A continuous cycle, with spermatozoa in seminiferous tubules and/or sperm in the epididymis during the entire activity season, was found in *L. pictus* (Ibargüengoytía and Cussac 1998), and in the southernmost reptiles of the world *L. sarmientoi* and *L. magellanicus* (Fernández et al. 2017), in populations with low availability of receptive females due to their multiennial prolonged cycle. A continuous pattern allows males to be ready for females throughout their entire unpredictable and short activity season (Ibargüengoytía and Cussac 1998; Fernández et al. 2017). In addition, in *L. sarmientoi* and *L. magellanicus,* spermatozoa occur in testes and the epididymis in spring and late summer, suggesting overwinter sperm storage to ensure the availability of males as soon as females are receptive (Fernández et al. 2017; Table 12.2), a selective advantage to deal with the harsh environmental restrictions that strongly affect the female cycle. Similarly, males of *L. pictus* living in montane forests in western Patagonia, Argentina, face a strongly skewed operational sex ratio (OSR, proportion of reproductive males-receptive females) due to the biennial to triennial reproductive cycle during the spring-autumn activity season (Ibargüengoytía and Cussac 1996, 1998).

Males of *L. elongatus* that are sympatric with *L. pictus* but are saxicolous reproduce during a narrower period during the activity season. Males exhibited spermatozoa in the seminiferous tubules in late spring and late summer (Ibargüengoytía and Cussac 1998; Table 12.2). The differences in the male reproductive cycles between *L. pictus* and *L. elongatus* were attributed to a difference in OSR due to low proportion of receptive females during the breeding season, a consequence of the difference between female reproductive cycles (Ibargüengoytía and Cussac 1998). Nevertheless, the differences between both species could be also attributed to the different access to thermal microenvironments, since *L. elongatus* bask on rocks that retain heat for longer periods and are usually more exposed to solar radiation. *Liolaemus pictus*, in contrast, occurs in shadier areas in the underbrush of the *Nothofagus* and *Austrocedrus* forests.

Another study of sympatric and syntopic species was focused on two populations at different latitudes of *Liolaemus bibronii* (oviparous), *Liolaemus boulengeri* (oviparous), and *Liolaemus lineomaculatus* (viviparous), in Esquel (Chubut Province, 43° S 70° W, 626 m a.s.l.) and Perito Moreno localities (Santa Cruz

Province, 46° S 71° W, 263 m a.s.l.; Medina and Ibargüengoytía 2010). Male reproductive cycles showed slight interspecific differences in the timing of spermatogenesis and in the relative duration of the regression stage, the latter occurring from midspring to the beginning of autumn in *L. bibronii*, from midspring to summer in *L. boulengeri,* and from late spring to midsummer in *L. lineomaculatus* (Table 12.2). However, all species showed a seasonal postnuptial reproductive pattern characterized by recrudescence from late spring to autumn, and some co-occurrence of males showing highest gonadal activity, as indicated by spermatozoa in testes and epididymis in early to midspring and in autumn, suggesting overwinter sperm storage, probably to make fertilization possible immediately after winter (Medina and Ibargüengoytía 2010). Similarly, there were no differences between the reproductive cycles of males at high- and low-latitude populations; in both locations, there were annual cycles and synchrony between males and females' reproduction (Medina and Ibargüengoytía 2010).

Male reproductive cycles can be considered as the functional counterpart of the male component of sexual dimorphism. In this sense, it has been proposed that in environments with strong thermal restrictions, vitellogenesis and pregnancy are highly constrained, resulting in complex causal relationships between female and male reproductive cycles, that also affect male dimorphic traits (Ibargüengoytía and Cussac 1996, 1998, 1999). The studies on reproductive biology of lizards from Patagonia, Argentina, support this statement, since it is clear that environmental and physiological cues (especially progesterone limitations in viviparous species; described in Sect. 12.3) constrain the female cycle leading to the evolution of multiennial prolonged cycles, skewing the OSR due to the low proportion of receptive females, and consequently affecting male reproductive cycles and the development of male sexual dimorphism. For example, an OSR biased toward males was found in *P. tenebrosus* (60–40; Ibargüengoytía 2004), *P. spectabilis* (= *P. spurcus*, 65–35; Boretto et al. 2014b), and *P. zapalensis* (72–28; Boretto 2009). In general, a male-biased OSR results in intrasexual competition among males, which in turn increases the risk of their predation (Sugg et al. 1995), and favors the evolution of dimorphic traits. Thereby, males of *P. zapalensis* (Boretto and Ibargüengoytía 2009), *P. tenebrosus* (Ibargüengoytía 2004), *P. spectabilis* (= *P. spurcus*, Boretto et al. 2014b), and *L. sarmientoi* (Fernández et al. 2017) exhibit relative larger head widths than females. Similarly, *L. magellanicus* exhibits a relatively larger head height than females (Fernández et al. 2017), and *L. bibronii*, *L. boulengeri,* and *L. lineomaculatus* exhibit a common pattern characterized by a larger head in males than females (Medina and Ibargüengoytía 2010). In addition, males of *P. zapalensis* exhibit greater neck width and diameter of the front leg and hind leg than females (Boretto and Ibargüengoytía 2009). These observations are consistent with the hypothesis of sexual selection via mate competition in male Patagonian liolaemids, in order to enhance success in male-male fights, due to the low proportion of receptive females in the population and the consequent male-biased OSR.

12.5 Hormonal Control of Reproduction in Males

Physiological function, including endocrine control mechanisms, mediates the relationship of the organism to its environment and therefore is essential to our understanding of the diversification of life histories (Ricklefs and Wikelski 2002). In previous sections, we have shown that lizards living in harsh and cold environments of Patagonia, Argentina, are energetically constraint and need to reproduce during the short activity season, since physiological activity during the long brumation is almost null (Saint Girons 1985; Gotthard 2001). In consequence, male and female reproductive cycles are under strong selection to increase the offspring's probability of survival during its first year (Saint Girons 1985; Olsson and Shine 1998; Gotthard 2001). So, Patagonian lizards show reproductive cycles timed to favor spring readiness and male-female encounters to attain early mating and fertilization, initiating growth and development of embryos without delay, and ensure that births occur during warmer periods of activity seasons. In this way, males have developed different paths to coordinate with female cycles, showing interspecific differences. Aside from these aspects, ultrastructural and endocrine studies have shown that some *Phymaturus* males have developed particular physiological mechanisms that allow them to synchronize with the female reproductive cycle (Boretto et al. 2010b, 2012, 2014c). In Patagonia, *Phymaturus zapalensis* males exhibit this physiological mechanism to synchronize with the female annual-biennial cycle (Boretto and Ibargüengoytía 2009). Males feature a postnuptial cycle, with a long period of spermatogenesis starting after copulation in midsummer, arrested during brumation in winter, and completed in midspring when the epididymis contains spermatozoa in synchrony with the female ovulation (Boretto and Ibargüengoytía 2009). In contrast with the general pattern for postnuptial cycles proposed by Pudney (1995), males of *P. zapalensis* do not retain sperm in the epididymis during brumation, and spermiation occurs only after winter brumation (Boretto and Ibargüengoytía 2009). These differences with the general pattern support their classification as a dissociated reproductive cycle, due to the long period of spermatogenesis temporally dissociated from mating, providing a particularly good cold-climate model to study the role of steroid hormones in the regulation of seasonal reproductive events.

The physiological mechanisms that allow male-female synchrony consist of asynchronous steroid hormone synthesis between Leydig and Sertoli cells from the interstitial and tubular compartments of the testes, respectively, making spermatogenesis temporally independent of mating, as was described initially in turtles (Callard and Ho 1980; Mahmoud et al. 1985; Dubois et al. 1988; Mahmoud and Licht 1997). Ultrastructural studies confirm steroidogenic activity of Leydig and Sertoli cells in male *P. zapalensis* (Boretto et al. 2012), as is indicated by the marked development of smooth endoplasmic reticulum, the abundance of mitochondria with tubular cristae, and a reduction of cytoplasmic lipid droplets where cholesterol is stored (Lofts and Tsui 1977; Dubois et al. 1988; Ibargüengoytía et al. 1999; Ferreira and Dolder 2003). Likewise, a marked accumulation of lipid droplets, a minor development of smooth endoplasmic reticulum, and a minor number of mitochondria with tubular cristae were recognized as an indicator of steroidogenic inactivity in Leydig and Sertoli cells (Callard et al. 1976; Lofts and Tsui 1977; Mahmoud et al. 1985; Dubois et al. 1988). Boretto et al. (2012) also determined the concentration of serum testosterone during the male reproductive cycle in *P. zapalensis*. Evidence of an alternate steroidogenic activity between testicular compartments, characterized by the presence of Sertoli cells with morphological signs of steroid synthesis and Leydig cells with morphological signs of steroid inactivity, was found in males of *P. zapalensis* captured in summer and autumn (Boretto et al. 2012). These males were developing a new spermatogenic cycle and exhibited spermatid or spermatozoa stages, without spermatozoa in the epididymis, and the concentration of serum testosterone was moderate. In contrast, during spring when testosterone peaks and mating occurs, the steroidogenic activity of Leydig and Sertoli cells was synchronous (Boretto et al. 2012).

The development of smooth endoplasmic reticulum in Sertoli cells, as indicator of steroidogenic activity, was described in liolaemids only in males of *Liolaemus darwinii* (Gutiérrez and Yapur 1983), *Phymaturus antofagastensis* (Boretto et al. 2010b), *Phymaturus zapalensis* (Boretto et al. 2012), and *Phymaturus punae* (Boretto et al. 2014c). In reptiles, Sertoli cells appear to have the potential to synthesize a variety of steroids, but it is clear that the contribution to the circulating androgen pool is minimal and their action is limited to the seminiferous tubules and is associated with the synchronization and maintenance of spermatogenesis (Bardin et al. 1988; Dubois et al. 1988). In contrast, Leydig cells synthesize androgens that enter into peripheral circulation, stimulating courtship behaviors and mating events (Dubois et al. 1988). These differences in testosterone availability and distribution between Sertoli and Leydig cells make possible the independence or temporal dissociation of spermatogenesis and mating (Mahmoud et al. 1985; Dubois et al. 1988; Mahmoud and Licht 1997). Such physiological mechanisms have particular importance in species that must cope with strong thermal constrains in their microenvironments (e.g., *P. zapalensis*; Duran et al. 2018) and that exhibit annual-biennial female cycles and consequently, low availability of receptive females that skew the OSR toward males (Boretto 2009). In consequence, these physiological and endocrine mechanisms synchronize male postnuptial reproductive cycles with female receptivity (Boretto and Ibargüengoytía 2009) because spermatogenesis is temporally dissociated from spermiation and copulation (Boretto et al. 2012).

Male serum testosterone concentration during the activity season has been studied in some viviparous species of the family Liolaemidae including *Liolaemus gravenhorsti,* which exhibits a postnuptial spermatogenic cycle (Leyton et al. 1977); *Phymaturus antofagastensis* (Boretto and Ibargüengoytía 2006; Boretto et al. 2010b) and *Phymaturus aguanegra* (Cabezas-Cartes et al. 2010), which shows a continuous and asynchronous spermatogenic cycle; and *P. punae*, a species with a prenuptial male cycle (Boretto et al. 2007; Boretto 2014c). But in Patagonia Argentina, only the hormonal cycle of *P. zapalensis* was studied, and their testosterone cycle parallels the annual and postnuptial spermatogenic cycle described previously (Boretto and Ibargüengoytía 2009). In this species testosterone concentration decreases abruptly in males after spermiation and mating, and the beginning of a new spermatogenic cycle is accompanied by a gradual increase in serum testosterone concentrations. The spermatogenic and testosterone cycles observed in males of *P. zapalensis* are possibly due to the temporal separation of steroidogenic activity of Leydig and Sertoli cells, since testosterone synthesized by Leydig cells in males during spring stimulates the beginning of activity in seminiferous tubules and a new spermatogenic cycle in early summer, whereas Sertoli cells maintain the progress of the spermatogenic cycle while Leydig cells are inactive (Boretto et al. 2012). This testosterone cycle ensures male readiness at the onset of female ovulation and the synchrony of males and females reproductive cycles in *P. zapalensis* (Boretto and Ibargüengoytía 2009; Boretto et al. 2012).

The section above describes a particular physiological mechanism present in, at least, one Patagonian species. It is necessary to extend this kind of study to a larger number of species with different patterns of male and female reproduction to understand hormonal control of male and female reproductive cycles. In addition, the incorporation of histochemical studies to evidence the presence of key enzymes, such as Δ^5-3β-hydroxysteroid dehydrogenase (3β-HSD) or 17β-HSD, is expected to add more support to morphological evidence of steroidogenic activity in Sertoli cells and their temporal asynchrony with the steroidogenic activity of Leydig cells.

12.6 Energy Allocation to Growth and Reproduction

The environmental harshness of the Patagonian steppe imposes great physiological demands over liolaemids, so lizards must balance very precisely the resources among vital functions which results in the existence of allocation trade-offs that occur whenever an organism divides a finite amount of resources between competing demands like growth or reproduction (Angilletta Jr 2009). The cold and low-energy environment of Patagonia where lizards inhabit, combined with prolonged female reproductive cycles and the low annual reproductive output, makes them an appealing model to study the evolution of energy allocation trade-offs between growth and reproduction. In order to analyze these trade-offs, it is essential to determine not only the reproductive biology of the species but also the life-history traits related to development, growth, and age, specifically age at maturity, growth rates, and longevity.

A very useful tool to determine individual ages and growth rates in reptiles is skeletochronology, a reliable and robust histological technique based on the study of annual growth rings in bones that appear in cross sections as broad layers followed by narrower, denser layers of arrested growth (LAGs) constituted of lamellar bone (see Castanet et al. 1993; Fig. 12.1). The broad layers are zones of growth, whereas the narrower layers signal periods of decreased growth rates (Peabody 1961). These LAGs are usually clear in seasonal species and indicate changes in climate, dietary resources, or both (Castanet 1985; Caetano and Castanet 1987). In consequence, in species from seasonal environments, a zone terminated by a LAG usually indicates a complete cycle of annual growth (Wake and Castanet 1995;

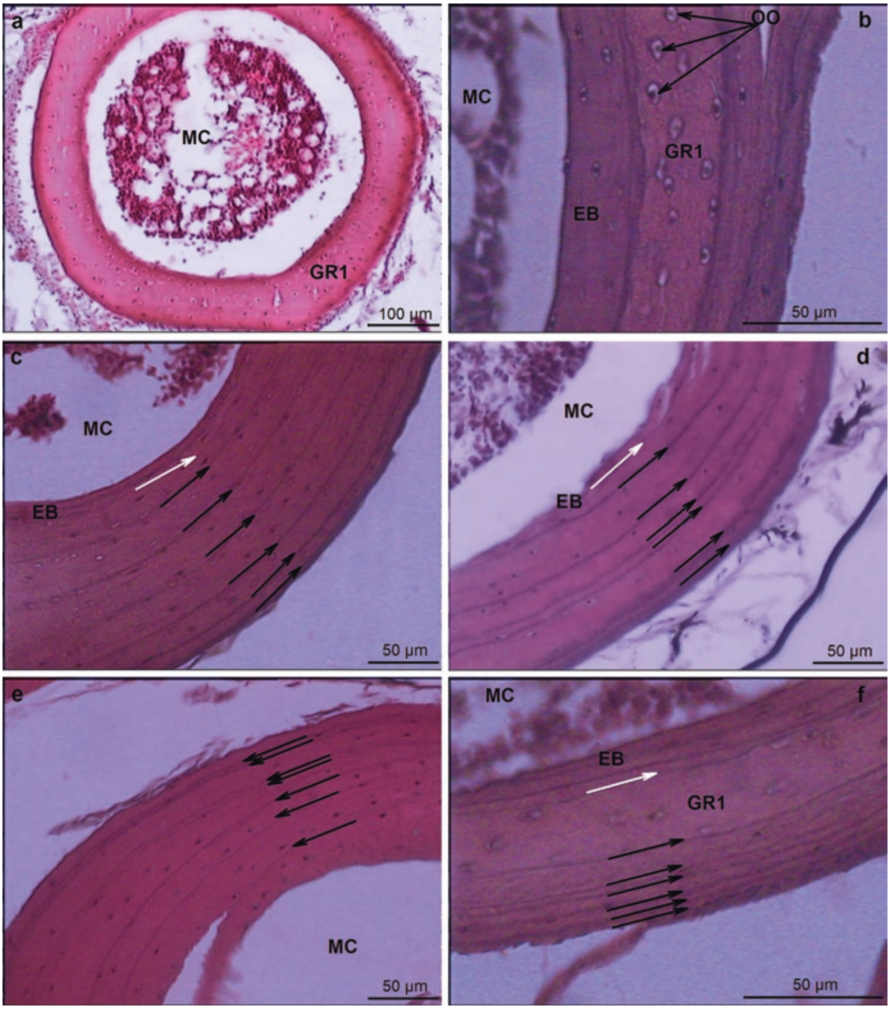


Fig. 12.1 Diaphysial cross section of femora stained with hematoxylin-eosin of different individuals of *Phymaturus* species of Patagonia: (**a**) female newborn of *P. zapalensis* showing a single embryonic growth ring at birth (*GR1*; ×100); (**b**) juvenile male of *P. spectabilis* (= *P. spurcus*) showing endosteal bone (*EB*) proximal to the marrow cavity (*MC*), line of resorption (*white arrow*), and osteocytes (*OO*; ×400); (**c**) adult female of *P. zapalensis* showing endosteal bone, line of resorption, and six lines of arrested growth (LAGs, *black arrows*; ×200); (**d**) adult male of *P. spectabilis* (= *P. spurcus*) showing endosteal bone, line of resorption, and six LAGs (×200); (**e**) adult female of *P. zapalensis* showing alternation of wider and narrower growth rings and seven LAGs (×200); and (**f**) juvenile male of *P. zapalensis* showing the embryonic bone plus the first activity season growth ring (*GR1*) and six LAGs (×400)

Piantoni et al. 2006a, b). Particularly, lizards are the most studied taxa given that they present a simple bone structure with low vascularization (except varanids that exhibit a complex vascularization), together with low intracortical remodeling and absence or rare supplementary marks (Castanet 1994). Specifically, lizards from cold-temperate regions are more suitable for skeletochronology than those inhabiting the tropics, since their growth rings are more marked as consequence of the greater decrease in metabolic activity produced by the low temperatures during cold seasons (Cagle 1950; Enlow 1969).

The studies of annual growth rings in bones provide valuable information about age at sexual maturity, longevity, and age-specific growth rate (Girons et al. 1989; Castanet and Báez 1991; Gutiérrez et al. 2013). Thus, when clutch size and reproductive cycles are analyzed in relation to longevity and age at maturity, inferences about life-history tactics in cold environments become possible (Boretto et al. 2018). In Patagonia, skeletochronology has shown that *Liolaemus pictus argentinus*, an insectivorous species of temperate forests (770–1770 m a.s.l.), mature relatively early at 3 years and live up to 9 years (Gutiérrez et al. 2013). The biennial-triennial female reproductive cycle results in a mean annual reproductive output of 1.8 offspring per female per year and a mean lifetime reproductive success of nine offspring per female (Gutiérrez et al. 2013; Table 12.3). In contrast, *Homonota darwinii,* a gecko that inhabits rocky outcrops in the Patagonian steppe, shows a very short reproductive life since it matures at 3 years and lives to only 7 years (Kubisch et al. 2012). Furthermore, the fecundity of this species is one of the lowest known in lizards (two offspring per female lifetime) a consequence of the biennial female reproductive cycle and the litter size of one offspring (Ibargüengoytía and Casalins 2007; Table 12.3).

One of the most surprising findings of skeletochronological studies of Patagonian lizards is the high rates of bone resorption. Such rates in Andean and Patagonian liolaemids are higher than in European lizards of similar body size and longevity (e.g., Roitberg and Smirina 2006; Guarino et al. 2010). These differences in the bone resorption could be attributed to greater physiological demands in Andean and Patagonian liolaemids than those of European cold-temperate environments. The longer periods of inactivity and more limited food availability might favor a relocation of minerals deposited in bones to other regions of the body, producing the high rates of bone resorption observed in Patagonian species (Boretto et al. 2018).

In the same way, the allocation of materials and energy to the different vital functions is reflected in the growth curves of the species. Like most other reptiles, juveniles from Patagonia grow faster than adults (Piantoni et al. 2006a, b; Kubisch et al. 2012; Gutiérrez et al. 2013; Cabezas-Cartes et al. 2015, 2018a), allocating energy primarily toward growth while adults shift energy toward reproduction (Kusano et al. 1995; Measey 2001; Wapstra et al. 2001; Bruce et al. 2002). In adults, the allocation of time, energy, and biomass for reproduction and brood care (reproductive effort; Stearns 2000; Charnov 2005) decreases the growth of somatic tissues (Pianka 1982; Stearns 2000). Lizards that live in cold-temperate climates delay age at sexual maturity, investing more prematuration energy into growth and maintenance, presumably to maximize future reproduction (Tinkle et al. 1970; Wapstra

Table 12.3 Age and size at sexual maturity, longevity, clutch/litter size, reproductive frequency, net reproductive rate (R_0), reproductive effort (RE), and lifetime reproductive effort (LRE) of Patagonian lizards

Species	Age at sexual maturity (years)	Size at sexual maturity (mm)	Longevity (years)	Clutch/ litter size	Reproductive frequency	R_0	*RE*	*LRE*
Phymaturus zapalensis[a,b]	♂ = 8 ♀ = 9	♂ = 75 ♀ = 79	♂ = 15 ♀ = 14	1–2	0.5–1	5.6	0.17	1.33
Phymaturus spectabilis (= P. spurcus)[c,d]	♂ = 6 ♀ = 7	♂ = 79 ♀ = 83	♂ = 11 ♀ = 12	1–3	0.5–1	7.5	0.25	1.26
Phymaturus tenebrosus[e,f]	♂ = 9 ♀ = 7	♂ = 87.2 ♀ = 90.2	♂ = 13 ♀ = 16	2	0.5	9	0.31	1.36
Liolaemus pictus argentinus (low altitude)[g,h]	♂ = 4 ♀ = 4	♂ = 49.8 ♀ = 51.7	♂ = 9 ♀ = 7	3–6	0.3–0.5	5.4	NA	NA
Liolaemus pictus argentinus (high altitude)[g,h]	♂ = 4 ♀ = 3	♂ = 51.4 ♀ = 50.4	♂ = 8 ♀ = 8	3–6	0.3–0.5	9	NA	NA
Homonota darwinii (Patagonian steppe)[i,j]	♂ = 3 ♀ = 3	♂ = 36.2 ♀ = 37.5	♂ = 7 ♀ = 7	1	0.5–1	2	NA	NA
Homonota darwinii (Patagonian Monte)[i,j]	♂ = 4 ♀ = 4	♂ = 41.3 ♀ = 47.1	♂ = 5 ♀ = 5	1	0.5–1	0.5	NA	NA

NA no data available, ♂ male, ♀ female

[a]Cabezas-Cartes (2016, 2018a); [b]Boretto and Ibargüengoytía (2009);[c]Cabezas-Cartes et al. (2015); [d]Boretto et al. (2014a, b); [e]Piantoni et al. (2006a); [f]Ibargüengoytía (2004); [g]Gutiérrez et al. (2013); [h]Ibargüengoytía and Cussac (1996); [i]Kubisch et al. (2012); [j]Ibargüengoytía and Casalins (2007)

et al. 2001; Roitberg and Smirina 2006). Accordingly, the species of *Phymaturus* in Patagonia mature at 6 to 9 years old (Piantoni et al. 2006a; Cabezas-Cartes et al. 2015, 2018a; Table 12.3), some of the oldest known ages at sexual maturity when compared to many other lizards around the world (Mesquita et al. 2015). The delayed sexual maturity of *Phymaturus* could be the result of the highly conservative life history of the genus, evolved under the environmental restrictions imposed by the harsh Patagonian or Andean environments (Cabezas-Cartes et al. 2018a).

Sexual maturity results in secondary sexual characters and sometimes sexual size dimorphism, which may result in larger and more successful males (van Devender 1978; Anderson and Vitt 1990; Verrastro 2004) or larger females that could produce larger or more litters or both (Tracy 1999; Smith 2002; Chamaille-Jammes et al. 2006; Pincheira-Donoso and Tregenza 2011). Greater reproductive output or larger newborns, or both, could be an important adaptive trait especially in cold-temperate environments where higher thermal inertia relative to body size can determine survival, mostly in newborns. In *Phymaturus* females, which exhibit larger inter-limb length than males, a larger abdominal size would allow offspring to reach a greater size at birth, increasing the survivorship (Olsson et al. 2002). The abundant fat reserves observed in the offspring of *P. spectabilis* (= *P. spurcus*, Boretto et al. 2014b), as well as the large fat bodies and intra-abdominal yolk reserves found in the offspring of *P. zapalensis* (Boretto and Ibargüengoytía 2009), give support to this prediction. Also, the reproductive investment observed in liolaemids of Patagonia highlights that reproduction would entail higher energy requirements in females than in males (Saint Girons 1985), and in consequence, lower growth rates would be expected in females. However, adult females of *P. spectabilis* from Ingeniero Jacobacci (Río Negro Province) presented higher growth rates than males (Cabezas-Cartes et al. 2015). In some reptiles, the energetic requirements for spermatogenesis are comparable to those required for courtship, copulation, and defense of the territory (e.g., the snake *Vipera berus*; Olsson et al. 1997), which would reduce growth rates in males as well. Besides, high growth rates of adult female *P. spectabilis* (= *P. spurcus*) could result in an increment in body size and mass of offspring, rather than increasing fecundity, as described in previous sections.

The production of offspring entails associated costs, usually known as "costs of reproduction" (Williams 1966; Shine 1980, 2005). One of the most used parameters to estimate these costs is the reproductive effort (RE), which is defined as the energetic equivalent of the proportion of adult biomass devoted to reproduction per unit of time (Charnov et al. 2007). Therefore, RE is measured as the fraction of body mass expended in reproduction per year, thereby involving trade-offs with other needs of the individual, such as investment in growth, maintenance, or energy storage (Stearns 2000; Charnov 2002), and is inversely proportional to average adult life span (Charnov 2005). In *Phymaturus*, there seems to exist a physiological compromise between the number of lifetime reproductive events and the reproductive effort devoted to each event (Boretto et al. 2018). Some Patagonian species like *P. tenebrosus* and *P. spectabilis* (= *P. spurcus*) exhibit higher REs but shorter reproductive life span and hence fewer reproductive events during life (Table 12.3; Cabezas-Cartes et al. 2018a). In contrast, *P. zapalensis* exerts a moderate RE but also few reproductive events (Table 12.3; Cabezas-Cartes et al. 2018a) which could affect negatively the recovery rate of populations that have suffered episodes of mortality, common in Patagonia, caused by disturbances such as fires, prolonged drought, and volcanic ashfall (Dubey et al. 2013; Cabezas-Cartes et al. 2014; Boretto et al. 2014a), reinforcing the vulnerability status of this species (Abdala et al. 2012).

Growth is comparatively costlier for lizards that live in environments where activity time is a limited resource, favoring not only late sexual maturity but also high longevity. In this sense, skeletochronological studies of *Phymaturus* species from Patagonia revealed the occurrence of medium to high longevities (12–16 years; Piantoni et al. 2006a; Cabezas-Cartes et al. 2015, 2018a). It has been suggested that longer-lived organisms typically exhibit lower RE (Stearns 2000; Charnov et al. 2007). Indeed, it has been stated that *Phymaturus* exhibited the lowest rate of specific productivity, defined as the total offspring mass produced per year in relation to the mother mass (*sensu* Meiri et al. 2012) when compared with other groups of reptiles. Nevertheless, recent life-history studies of the *Phymaturus* species from Patagonia like *P. tenebrosus* and *P. spectabilis* (= *P. spurcus*) demonstrated that they allocated 31% and 25%, respectively, of their biomass in reproduction per year (Table 12.3; Cabezas-Cartes et al. 2018a), which represents a reproductive effort by unit of time higher than the median for viviparous lizards (21%; Meiri et al. 2012).

12.7 Parental Care

Reproductive investment involves not only the energetic costs of gametogenesis and embryogenesis, but also in some species includes the effects on fitness associated with parental care, in its many ways (Low 1978). Parental care can be defined as those behaviors that increase the fitness of offspring by providing protection and/or nutrition (Pike et al. 2016). Harsh environmental conditions, high predation pressure, and resource competition have been pointed out as the main driving forces behind the evolution of parental care (Shine 1988; Clutton-Brock 1991; Pike et al. 2016). Since Patagonia is a region characterized by low temperatures, restricted activity periods, a paucity of resources, and possibly high predation pressure due to open habitats, the lizards of this region are good candidates to study parental care. Besides, in Patagonia, many species of *Liolaemus* and all *Phymaturus* are viviparous, a reproductive mode that has recently been associated with the evolution of sociality in squamates (Halliwell et al. 2017). Viviparity may favor the development of parent-offspring interactions by increasing the recurrence of physical association between parents and neonates (Lion and van Baalen 2007; Davis et al. 2011; Klug et al. 2012), or by facilitating kin recognition via prolonged physiological exchange between mothers and offspring throughout pregnancy (Itonaga et al. 2012; Blackburn 2015).

Patagonian lizards display a diverse repertoire of behaviors related to parental care. For example, in *Liolaemus kingii,* a medium-sized viviparous species that inhabits the steppes of central Patagonia, females assist their offspring at birth pushing them out using their hind legs and thus also breaking the amniotic sac (Ibargüengoytía et al. 2002). Also, females remain in contact with their offspring immediately after birth and tongue-flick them probably as a means of imprinting individual identity and recognition (Ibargüengoytía et al. 2002). The close perinatal association between mother and offspring has been proposed as an indirect form of parental care (Halloy et al. 2005) and was also registered in *Liolaemus elongatus*, a viviparous species that lives in rocky environments of the Patagonian steppe from Neuquén to Santa Cruz Province. Mothers and offspring of this species were found sharing the same shelter during the whole period of captivity after birth (Halloy et al. 2007). Such familiarity may help the neonates to thermo- and hydro-regulate (e.g., Somma 2003; Greene et al. 2006) during the cold, dry nights of Patagonia, in addition to the protection that mothers may provide (Halloy et al. 2007). When confronted with predation stimuli, mothers adopted different strategies to protect offspring, which may depend on the individual perceptions of the immediate threat: while some mothers remain near the shelter where offspring are hiding, others simply moved away possibly as a distractive behavior, as has been observed in some birds (Bergrstrom 1988; Canevari et al. 1991).

The behavioral repertoire of parental care can also be related to the type of predatory stimulus. For example, in *Phymaturus spectabilis (= P. spurcus)*, an endemic species of rocky outcrops of southwest Río Negro, different strategies were observed in presence of terrestrial versus aerial predators (Cabezas-Cartes et al. 2018b; Fig. 12.2). On the one hand, in the presence of a carnivorous lizard (*Pristidactylus nigroigulus*), a higher frequency of active antipredator behaviors such as head bobs, tail waves, and flights was registered. The higher frequency of head bobs by the mother might be interpreted as a signal to offspring of the potential predation threat, but also could function as a dissuasive signal to the predator, as could tail waving, communicating the prey's ability to escape and a lower likelihood of successful capture and handling of prey (hypothesis of pursuit-deterrent signal; Hasson 1991; Caro 1995). On the other hand, when the predation stimulus came from the air (a stuffed hawk, *Elanus leucurus*), females reduced exploration and activity and spent more time in close proximity to their offspring (less than 9 cm away). The freezing behavior can be interpreted as an antipredator behavior, as observed in other species of lizards (Vitt and Congdon 1978; Schwarzkopf and Shine 1992), while the close association between mother and offspring for a prolonged period has been proposed as an indirect form of parental care as mentioned above. Field observations confirmed that these types of behaviors are common in the natural environment of the species (Cabezas-Cartes 2016).

Evidence of parental care behavior recorded for *Phymaturus* (Halloy et al. 2005, 2013; Cabezas-Cartes et al. 2018b) reflects the relevance of these behaviors for enhancing offspring survivorship in the genus and suggests the idea of a common pattern of parental care and sociality in *Phymaturus*. It has been proposed that the evolution of family living depends on ecological and life-history characteristics that coevolve to bias the cost-benefit trade-off of delayed dispersal and create demographic conditions that favor philopatry and, thus, cooperative behavior among kin (Hatchwell 2009; Duffy and Macdonald 2010). In *Phymaturus*, the combination of delayed sexual maturity and greater longevity (see Sect. 12.6) that favor natal philopatry, together with the high fidelity to microhabitats that promote social contact on spatially aggregated resources (rock crevices; Cabezas-Cartes et al. 2014), could facilitate the emergence of social grouping (Whiting and While 2017). In fact, it is common to find "families" in crevices composed of a couple and juveniles sharing the same shelter (personal observations). Davis et al. (2011) suggest that viviparity promotes prolonged interactions between the mother and neonates which allow juvenile philopatry, resulting in extended social interactions, similarly to avian and mammalian systems. It is worth mentioning that this could be related to the fact that almost every isolated volcanic outcrop, where these lizards inhabit, seems to represent an independent evolutionary unit or species (Chap. 9). Further

Fig. 12.2 Female of *Phymaturus spectabilis* (= *P. spurcus*) carrying her offspring on her back, a common parental care display observed in *Phymaturus* and *Liolaemus* from Patagonia. Photo by María Soledad Ausas

research should focus on behavioral, genetic, and physiological performance and the relatedness of individuals in social groups to analyze the cost and benefits of sociality in these species and confirm this hypothesis.

12.8 Effects of Acute Environmental Stressors on Reproduction and Body Condition of Lizards from Patagonia

Much of the variation in life histories, particularly variation in parental investment and self-maintenance, reflects phenotypic responses of individuals to environmental stressors and perceived risks. As a result, the organization of behavioral and physiological control mechanisms might constrain individual and evolutionary responses and limit life-history variation among species (Ricklefs and Wikelski 2002). The last eruption of the Puyehue-Cordón Caulle Volcanic Complex beginning June 4, 2011, provided a valuable opportunity to study the effects of an acute environmental stressor on the reproductive cycle and body condition of Patagonian lizards. In particular, a population of the endemic viviparous lizard *P. spectabilis (= P. spurcus),* a species with vulnerable conservation status (Abdala et al. 2012) that inhabits an environment severely affected by ashfall in Ingeniero Jacobacci (Río Negro Argentina, Fig. 12.3b), was studied, because this population was observed previously during its activity seasons from 2006 to 2011. Their reproductive biology was described based on morphological and histological analysis of gonads and noninvasive techniques (abdominal palpation), registering data about body conditions of individuals and marking a large part of the individuals in the population for mark-recapture studies (Boretto et al. 2014b). As was described before, female *P. spectabilis (= P. spurcus)* display an annual-biennial reproductive cycle, while male shows an annual, seasonal, postnuptial cycle (Boretto et al. 2014a). Males are ready to mate during the spring months, and gestation occurs from midspring until late summer, when each female gives birth to two offspring (Boretto et al. 2014a). But following the volcanic eruption, these patterns changed.

Fig. 12.3 (**a**) Photograph of a *Phymaturus tenebrosus* climbing a rock covered with volcanic ash taken 7 months after the Puyehue-Cordon Caulle eruption. Photo by Nora Ibargüengoytía. (**b**) Photograph of a *Phymaturus spectabilis* (= *P. spurcus*) walking over volcanic ash 22 months after the Puyehue-Cordon Caulle eruption. Photo by Facundo Cabezas-Cartes

The eruption of Puyehue-Cordón Caulle complex dispersed about 100 M tons of pyroclastic materials onto the Patagonia steppe of Argentina due to the predominant westerly winds (Gaitán et al. 2011; Chap. 4). This natural catastrophic event was a significant disturbance of ecological native communities (Buteler et al. 2011; Grosfeld and Puntieri 2011; Huerta 2011; Ghermandi and González 2012; Martínez et al. 2012; Fernández-Arhex et al. 2013; Morales et al. 2014), since approximately 65 tons of ash materials have been deposited per ha from the city of San Carlos de Bariloche in the West to Pilcaniyeu to Ingeniero Jacobacci in the East (Río Negro Argentina; Gaitán et al. 2011). Also, climatic changes were documented in precipitation and temperature after the eruption (Boretto et al. 2014a). Precipitation decreased and the drought was extended even into the second year after the eruption. The great amount of ashes deposited in the field (up to 30 cm depth) and low precipitations limited the incorporation of ash into the soil, causing a strong impact on vegetation, reducing the presence of plant species in gaps and the recruitment of annual and matrix-dominant species (Ghermandi and González 2012). Likewise, an insecticidal effect of the ash was confirmed, reducing insect community, for insect host plants, and pollination rates (Buteler et al. 2011; Huerta 2011; Martínez et al. 2012; Fernández-Arhex et al. 2013). Additionally, changes in climatic conditions resulted in lower-minimum temperatures, and the number of activity hours available to lizards decreased during the first and the second activity season after eruption (Boretto et al. 2014a). This drop in activity time was likely due to the suspension of ash in the atmosphere, absorbing and reflecting solar radiation that *Phymaturus* lizards would normally use for basking to maintain activity body temperatures.

The negative impact of ash documented on climate, vegetation, and insects affects the ecology of both herbivorous and insectivorous lizard populations. For example, the negative effects of ash on running performance were confirmed in three endemic and vulnerable species of genus *Phymaturus* (Cabezas-Cartes et al. 2014; Ibargüengoytía et al. 2016) restricted to volcanic rock outcrops in Patagonia, Argentina. The presence of volcanic ash on the substrate (Fig. 12.3) affects lizard locomotor performance, with consequences for their interaction with the environment, evasion of predators, and social behavior (Cabezas-Cartes et al. 2014; Ibargüengoytía et al. 2016). In the same way, this acute environmental stressor caused detrimental effects on reproduction of lizards. Specifically, this catastrophic event affected the female reproductive cycle and reduced clutch size and the body condition of newborn, juvenile, and adult *P. spectabilis* (= *P. spurcus*, Boretto et al. 2014a). Before the Puyehue-Cordón Caulle eruption, 59% of adult females were vitellogenic or gravid during each activity season (Boretto et al. 2014b), whereas the rate was only 12% during the first activity season after ashfall. The only gravid female captured post-eruption in summer 2012, kept in laboratory until mid-autumn, did not give birth, suggesting a delay in parturition date that, if generalized to the population, would be detrimental for the offspring's first-year survival (Boretto et al. 2014a). The majority of females skipped reproduction clearly as a mechanism to cope with the detrimental changes caused by ash deposition reducing feeding rates and body condition. Low food availability and variation in nutritional content decrease the concentration of calcium in the organisms, affecting growth rates as well as reproductive processes like vitellogenesis, with attendant effects on reproduction (Lagarde et al. 2003).

However, a rapid recovery during the second activity season post-eruption and previously unreported plasticity in litter size were registered in *P. spectabilis (= P. spurcus)*. A great proportion of adult females (87%) were reproductive, and gravid females gave birth as they normally would in midsummer. Also, body conditions of juveniles and adult males were higher than during the first activity season post-eruption (Boretto et al. 2014b). But some negative effects persisted during the second activity season. For example, the clutch size changed from a fixed two individuals before eruption to a variable one to three individuals after eruption, being better the body condition of offspring born before eruption (summer 2011 versus summer 2013; Boretto et al. 2014b). In some lizard species, it has been documented that females could change their clutch size by changing the rate of follicular atresia in response to both intrinsic (female body size, amount of energetic reserves, specific hormonal concentrations) and extrinsic factors (availability of food, acute changes in the environment that cause stress; Méndez de la Cruz et al. 1993). In *Phymaturus*, rather than follicular atresia, the most common mechanism observed has been the variation in the number of follicles recruitment (Boretto and Ibargüengoytía 2006, 2009; Boretto et al. 2007, 2014b). Low offspring body condition showed that females could not invest the same amount of energy in reproduction. The significant regrowth of vegetation that occurred 17–20 months post-eruption and the removal of ash from rocky outcrops by wind (personal observation) probably were factors that permitted normal locomotion and a resumption of feeding opportunities that could explain the recovery in female reproduction and body condition of *P. spectabilis (= P. spurcus)*.

It is clear that plasticity in female reproductive frequency, manifest as changes in the proportion of females reproducing, is a coping mechanism to unpredictable climates or acute environmental disturbances. In species with strictly biennial female reproduction, it is expected that post-disturbance recovery in female reproduction takes more time, at least 2 to 3 years. Assuming that feeding opportunities are limited, females must devote one season to recover the minimum body condition that allows them to reproduce and then perform vitellogenesis in the second activity season and gestation in the third. In contrast, species with flexibility in frequency of female reproduction and an annual-biennial cycle, such as that in *P. spectabilis* (= *P. spurcus*), could skip reproduction in the year immediately following disturbance to maintenance of body condition and store energy reserves, and then execute vitellogenesis and gestation in the next favorable activity season.

12.9 Final Considerations and Future Directions

The fundamental knowledge of the ecophysiological adaptations to hard climatic conditions in those reptiles that inhabit high latitudes and altitudes allows the understanding of reproductive diversity (Tinkle and Gibbons 1977; Shine 1985; Blackburn 1993) and the possible physiological responses to their changing environment. This chapter showed that some lizards living in cold climates of Patagonia, Argentina, have evolved different reproductive strategies, yet other species remain unstudied. The importance of prior and detailed knowledge of the reproductive biology of a species was revealed, for example, when it was necessary to assess the impacts of Puyehue-Cordón Caulle eruption on the reproductive cycle and the body condition of *P. spectabilis* (= *P. spurcus*, Boretto et al. 2014a). Likewise, the knowledge of reproductive cycles of species was crucial when specialists from different Argentinian institutions contributed biological, ecological, geographical, and taxonomic information to reevaluate the conservation status of the 256 lizard and amphisbaenian species from Argentina (Abdala et al. 2012). For the categorization of those species, the existence of prior information on the reproductive biology of *Phymaturus* species combined with the precise age at sexual maturity and longevity, attained by skeletochronology, allowed researchers to categorize the genus as Vulnerable in terms of conservation status (Abdala et al. 2012).

In *Phymaturus*, the study of energy allocation between growth and reproduction in cold and constraining environments revealed slow and conservative life histories (Boretto et al. 2018). The delay in the age at sexual maturity to invest energy into growth and maintenance, in order to maximize future reproduction, situates *Phymaturus* species alongside those with the oldest ages at sexual maturity of lizards worldwide (Mesquita et al. 2015; Boretto et al. 2018). However, despite the value of this knowledge in the context of species conservation, only five species of lizards of Patagonia have been studied in this regard.

The integrated review of the present chapter shows that reproductive cycles of Patagonian lizards favor male-female encounters, and even when oviparous and viviparous species and differences in male and female cycles were found, in all species, hatching and birth occur during warmer periods in summer season, maximizing growth trajectories of juveniles prior to their first winter. Additionally, a high parental investment per offspring, denoted by the presence of large fat bodies and intra-abdominal yolk reserves, was found in several Patagonian species to serve as a valuable energetic resource that probably ensures offspring survival (Crocco et al. 2008; Boretto and Ibargüengoytía 2009; Boretto et al. 2014b). This physiological strategy of energy stored has also been poorly explored in Patagonian lizards, and its relationship with the evolutionary transition from oviparity to viviparity remains to be explored. Indeed, placental structures were studied in only one viviparous species, *Liolaemus elongatus* (Crocco et al. 2008). The cost of providing energetic reserves to offspring, together with the costs of being viviparous, and to display maternal care behaviors, highlights the high parental investment performed by females of some *Liolaemus* and *Phymaturus* species from Patagonia (Ibargüengoytía et al. 2002; Halloy et al. 2005, 2007; Cabezas-Cartes et al. 2018b), undoubtedly necessary for the survival of the young in these constraining environments. Although they are still scarce, these studies show the existence of parental care strategies, in both behavioral and physiological form that ensure the provision of energy resources to newborns survivorship until they start feeding themselves (Crocco et al. 2008). It is probable that lizards of Patagonia have evolved a diversity of physiological and behavioral strategies to ensure offspring survival that have not been investigated yet. Indeed, the association between the viviparous reproductive mode and the evolution of social behaviors recently confirmed in Squamata (Halliwell et al. 2017) becomes particularly interesting to study in liolaemids of Patagonia (see Fernández et al. 2018), in convergence with the kin-based social interactions as other reptiles, birds, and mammals (Davis et al. 2011).

Few studies exist on the reproductive cycles of oviparous species living in Patagonia, and only preliminary studies have been made on the endocrine control of reproduction in viviparous lizards. For example, the postnuptial and dissociated male reproductive cycle has evolved numerous times in several reptile families (Whittier and Tokarz 1992), and in Patagonia, Argentina, the postnuptial cycle is the most frequent reproductive strategy. Nevertheless, the male hormonal cycle, and the underlying physiological cellular mechanism that permits it, was studied only in *Phymaturus zapalensis*, confirming the dissociated pattern (Boretto et al. 2012). In *P. zapalensis*, alternating steroidogenic activity between the Leydig cells in the interstitial compartment of the testis and the Sertoli cells in the tubular compartment of the testis allowed spermatogenesis to be temporally independent of mating (Boretto et al. 2012). In other Patagonian species, males evolved a continuous reproductive cycle and dimorphic traits to win male-male combats, as a response to a strongly skewed OSR toward males caused by the prolonged female cycles. Males are thus always ready to mate when females are receptive (Ibargüengoytía 2004; Ibargüengoytía and Casalins 2007; Boretto and Ibargüengoytía 2009; Boretto et al. 2014b; Fernández et al. 2017, 2018). Clearly, males of lizard species of Patagonia precisely synchronize with female cycles developing different patterns.

The understanding of the physiology underlying reproduction, growth, and behavior is increasingly important for the decision-making in conservation and management of the biota and its environment. Ecophysiological knowledge is being incorporated more often into ecological models to improve predictions of organism responses to environmental change and to provide tools to support management decisions (Cooke et al. 2013). Accordingly, we could determine the effects of increasing environmental temperatures on fertility, growth, phenology, age at sexual maturity and longevity, and their short-term and long-term consequences on population viability. For example, higher environmental temperatures are expected to extend the activity season and affect the timing of reproductive events with direct implications for energy allocation strategies, molding growth trajectories and trade-offs in investment in offspring number and body size. If lizards respond to global warming with increased growth rates, it could result in a concurrent reduction in longevity affecting the dynamics of the populations, as has been found for other species (Bestion et al. 2015). In this sense, it is necessary to increase the knowledge of the principal characteristics of the reproductive cycles of males and females, as well as their endocrine control, in a greater number of lizard species of Patagonia, to allow the prediction of the effects of environmental stressors and endocrine disruptors on individual performance and population status. Thus, the understanding of the developing cause-effect relationships would allow the identification of the optimal range of habitats and permit the definition of stressor thresholds that organisms may be able to afford (Cooke et al. 2013). All the studies that we reviewed here showed a great diversity of male and female reproductive cycles, life histories, physiological mechanisms that synchronize male and female cycles, levels of parental care, and responses to environmental stressors, but considering the large number of unstudied species, we highlight the importance of future research in Patagonia.

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Chapter 13
Effects of Acute and Chronic Environmental Disturbances on Lizards of Patagonia

Nora R. Ibargüengoytía, Erika Kubisch, Facundo Cabezas-Cartes, Jimena B. Fernández, Fernando Duran, Carla Piantoni, Marlin S. Medina, and Barry Sinervo

Abstract The extent of stress caused by acute and chronic environmental disturbances depends on the adaptive ability of organisms to behaviorally and physiologically adjust to change and on the timing and magnitude of the disturbances. This resilience is a result of numerous exposures to perturbations throughout the evolution of the species. In Patagonia, volcanic eruptions have caused larger and variable perturbations on populations and communities. The 2011 eruption of the Puyehue-Cordón Caulle volcano dispersed 100 M tons of pyroclastic material and accumulated ash layers of 30 cm. At the same time, a gradual but chronic increase in temperature, intensified by ozone depletion, affected especially taxa sensitive to thermal fluctuations. Nevertheless, species from cold temperate environments like Patagonia and the Andean mountains could benefit from warming as their body temperatures are commonly below preferred and optimum temperatures for performance. Eventually, cold temperate environments may provide refuge for northern or lowland species that while shifting their geographic ranges will potentially impact

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N. R. Ibargüengoytía (✉) · E. Kubisch · F. Cabezas-Cartes · J. B. Fernández · F. Durán
Instituto de Investigaciones en Biodiversidad y Medioambiente, Consejo Nacional de Investigaciones Científicas y Técnicas (INIBIOMA-CONICET),
San Carlos de Bariloche, Río Negro, Argentina
e-mail: norai@comahue-conicet.gob.ar; jimenafernandez@comahue-conicet.gob.ar; fernandoduran@comahue-conicet.gob.ar

C. Piantoni
Physiology Department, Bioscience Institute, University of São Paulo, São Paulo, Brazil

M. S. Medina
Centro de Investigación Esquel de Montaña y Estepa Patagónica, Consejo Nacional de Investigaciones Científicas y Técnicas (CIEMEP-CONICET), Universidad Nacional de la Patagonia San Juan Bosco, Esquel, Chubut, Argentina

B. Sinervo
Department of Ecology and Evolutionary Biology, University of California,
Santa Cruz, CA, USA

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local populations by competing for resources and transporting novel pathogens. In this chapter, we summarize studies on physiological traits of Patagonian lizards and discuss the biotic and abiotic factors involved in the evolution of these species. We integrate concepts of thermal biology, analyzing the relationship between the immune system and body temperature, and examining the thermal sensitivity and plasticity of locomotion, development, and growth rates using different geographic and temporal scales. The complex interplay of the ecophysiological strategies in Patagonian lizards is discussed based on their legacy of survival, having withstood and recovered from the extreme thermal fluctuations and catastrophic events for over ~140 Ma.

Keywords Liolaemidae · Volcanic ash · Climate Change · Lizards · Ecophysiology · Extinctions

13.1 Acute and Chronic Disturbances on Lizard Populations

Organisms respond to acute and chronic disturbances according to their resilience and to the magnitude of environmental impacts (Ruggiero and Werenkraut 2014; Mora and Labra 2017; Wild and Gienger 2018). Stressful environments can influence genotypic variability, via mutation and recombination, providing a source of new variation upon which natural selection can act, optimatizing plastic responses to environmental conditions (Hoffmann and Parsons 1997; Badyaev 2005; Wild and Gienger 2018). For example, genes controlling the expression of novel characters can be activated when the environment is stressful but downregulated under optimal environmental conditions conferring resilience to populations (Hoffmann and Parsons 1997).

Lizards from Patagonia on either side of the Andes experience interrelated acute and chronic disturbances (Boretto et al. 2014; Cabezas-Cartes et al. 2014; Ibargüengoytía et al. 2016; Mora and Labra 2017). Acute disturbances, such as volcanic eruptions and long droughts, can occur alone or in concert, affecting fire frequency in the Patagonian steppe and forests (Veblen et al. 2003). Key chronic disturbances are global warming and ozone layer depletion, both becoming more noticeable in Patagonia, particularly over the past 20 years (Barros et al. 2014). The expected increase in temperature for the coming decades will occur at twice the speed of the last 60 years, and precipitation is expected to be dramatically reduced, especially in western Patagonia (Barros et al. 2014).

However, the environmental challenges that Patagonian lizards have experienced, such as high fluctuation of temperature over the last 100 million years, suggest that many species could have a legacy of resilience that allows them to cope with these anthropogenic and natural environmental changes in diverse ways. Whereas individuals may adjust through phenotypical plasticity (Gause 1947; Bradshaw 1965; Wild and Gienger 2018) through buffer mechanisms such as modifying certain behaviors (thermoregulation), the timing for different tasks, or the diet and associated physiological processes, populations will depend on their genetic variability and capacity of adaptation to cope with change (Via and Lande 1985). However, if plasticity and adaptation are insufficient to keep pace with chronic change, organisms might instead shift, when possible, their geographic range to more suitable environments (Bonino et al. 2015, Minoli and Avila 2017, Minoli et al. 2019).

When exploring new environments is not an option, organisms must face the environmental disturbances that, at an individual level, may result in temporary but reversible ecophysiological responses (Boretto et al. 2014) involving aspects of life history (Warner and Shine 2008; Fernández et al. 2017) and potentially causing retraction and extirpation of local populations (Bestion et al. 2015). Lizards are constantly exposed to biotic (e.g., predators, competitors) and abiotic (e.g., large-scale disturbances) pressures that threaten their survival. Floods, drought, volcanic eruptions, hurricanes, and severe fires can be critical as they modify habitat and cause mortality and potentially local extinction (Lugo 2008; Elizalde 2014). In the last century, anthropogenic activities have enhanced climate change as well as the frequency in which these disturbances occur (Van Aalst 2006). In this regard, research on the effect of acute and long-term changes in the environment on organisms has become of paramount importance in biological conservation (Van Aalst 2006; Podolskiy 2009; Huang and Cheng 2013).

13.2 Effects of Volcanic Ash on Lizard Populations

In Patagonia, episodic volcanic activity has been prominent since the initial uplift of the Andes (Castro and Dingwell 2009). At present, there are many active volcanoes in the region (Dzierma and Wehrmann 2012) frequently producing pyroclastic ash during the Holocene (Singer et al. 2008; Stern 2008). Volcanic eruptions can modify entire landscapes through a diversity of geophysical disturbances including the precipitation of ash or tephra that may cover extensive areas (e.g., Mount St. Helens, >100,000 ha; Dale et al. 2005). As a consequence, in Patagonia, ashfall is not only a recurrent disturbance but also a medium- to long-term disturbance because ash remains in the environment for several years and its remobilization can be a dominant feature of posteruptive landscapes (Ayris and Delmelle 2012).

Particulate ash can have negative health effects on both animals and plants (Marske et al. 2007; Unno et al. 2014). In plants, the accumulation of ash on leaves induces damage that reduces photosynthetic activity (Seymour et al. 1983; Biondi et al. 2003; Ayris and Delmelle 2012) and, therefore, plant productivity (Tognetti et al. 2012; Chaneton et al. 2014). Also, insect-dependent plant reproduction can be negatively affected because pollinators are not able to locate flowers covered by ash (Morales et al. 2014). Insecticidal effects on herbivorous insects were also observed in the aftermath of some eruptions, which was attributed to dehydration, mechanical abrasion of cuticles, and accumulation of ash in their digestive and respiratory systems (Edwards and Schwartz 1981; Gersich and Brusven 1982; Buteler et al. 2014;

Elizalde 2014; Chaneton et al. 2014; Fernández-Arhex et al. 2013, 2015). In addition, those organisms that survive an eruption must face a radically changed environment in which much of their food is buried or covered with volcanic ash (Elizalde 2014; Fernández-Arhex et al. 2017). It has been reported that vertebrates also experience adverse effects attributable to the food shortage and difficulties in finding food in an ash-covered landscape (Wilson et al. 2011a, b; Pedersen et al. 2012).

Some Patagonian lizard populations seem to be well adapted to cope with the effects of intermittent eruptions during the last 11,500 years (Singer et al. 2008; Stern 2008). The massive eruption of the Puyehue-Cordón Caulle volcanic complex (2236 m a.s.l., 40° S; 70° W) in June of 2011 was a great opportunity to analyze the responses of lizard populations to this kind of disturbance. This particular eruption affected a considerable part of Patagonia, expelling into the atmosphere large amounts of pyroclastic material of variable particle size and texture that, due to the prevailing westerly winds, were deposited in an eastern trajectory toward the Atlantic Coast (Cremona et al. 2011; Gaitán et al. 2011). Several hundred million tons of volcanic tephra were dispersed over c. 25,000 km^2, along a west-to-east gradient (Gaitán et al. 2011) of the Argentine provinces of Neuquén, Chubut, and Río Negro and reaching areas just south of Buenos Aires (Bermudez and Delpino 2011). The locality of Ingeniero Jacobacci, in Río Negro, was one of the most affected sites (Fig. 13.1). This area is characterized by a high diversity and abundance of lizards, especially of the genus *Phymaturus* (Scolaro 2006; Perez et al. 2011; Chap. 9).

Studies of *Phymaturus* populations performed before and after the eruption were used to analyze the effect of ash deposition and relative abundance of predators on ecophysiological parameters related to fitness and survivorship, such as reproductive output (Boretto et al. 2014) and running performance of lizards (Cabezas-Cartes et al. 2014; Ibargüengoytía et al. 2016). Studies conducted during the first-year posteruption found that ash reduced sprint speed decreasing the locomotor performance of *Phymaturus excelsus* (= *P. spurcus*) (Ibargüengoytía et al. 2016) and was detrimental to locomotor performance, reproduction, and body condition of *P. spectabilis* (= *P. spurcus*) (Boretto et al. 2014; Cabezas-Cartes et al. 2014). Specifically, the negative effect on body condition was related to changes in the abundance of insects (Buteler et al. 2011; Morales et al. 2014; Fernández-Arhex et al. 2013, 2014) and food availability (Siffredi et al. 2011; Ghermandi and González 2012). However, an unexpected result showed that long-term effects of ashfall produced a decrease in the abundance of predators that feed on lizards and a decrease in herbivores that compete with lizards (Butcher 1981; Arendt et al. 1999; Dalsgaard et al. 2007). As a consequence, populations of *P. excelsus* and *P. spectabilis* (= *P. spurcus*) exhibited better body conditions and larger litter sizes in the second-year posteruption (Boretto et al. 2014; Ibargüengoytía et al. 2016; Chap. 12). The dramatic recovery of the population was probably the result of the increased availability of flowers and fruits resulting from the high mortality of livestock (i.e., sheep and goats), caused by the abrasive effects of ash on their intestines (Robles 2011; Boretto et al. 2014).

The environment can be tragically modified sometimes, but lizards seem to be resilient to this extreme impact on the ecosystem. Another example corresponds to

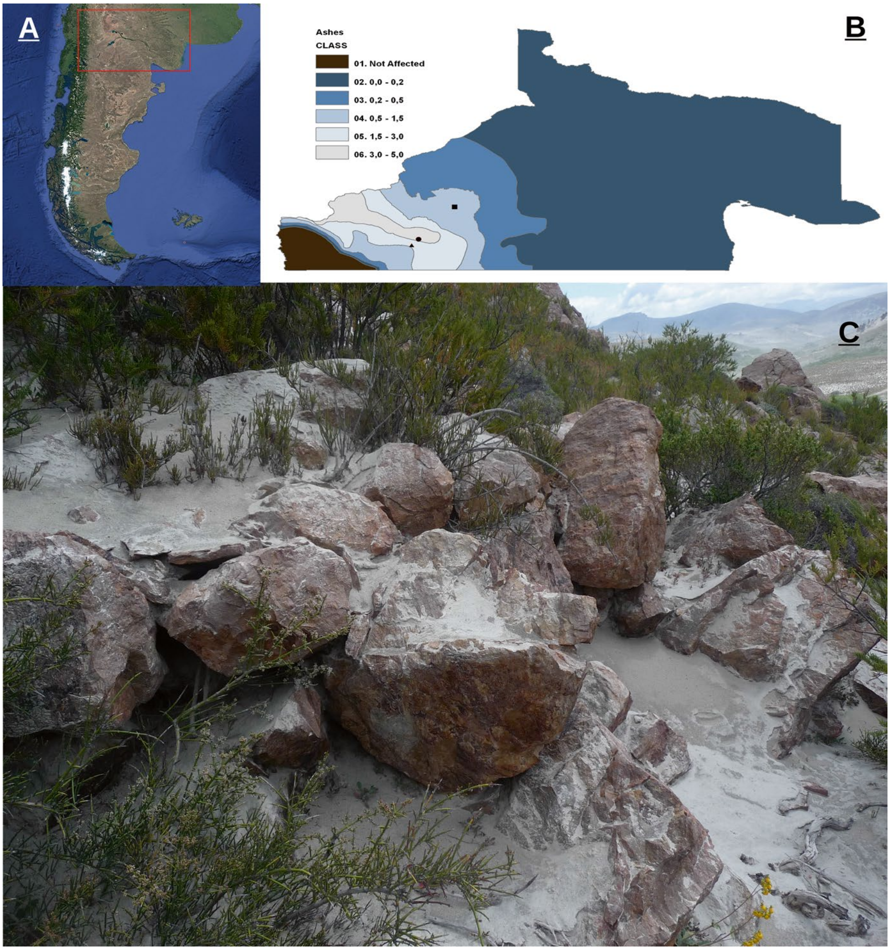

Fig. 13.1 (**a**) Relative situation of Río Negro Province in the context of Patagonia. (**b**) Map of Río Negro Province showing the amount of ash deposited (cm) in *Phymaturus* localities near Ingeniero Jacobacci (square *P. sinervoi* locality; triangle *P. excelsus* (= *P. spurcus* Barbour 1921, *sensu* Becker et al. 2019) locality; studied in Ibargüengoytía et al. 2016) and the locality of *P. spectabilis* (= *P. spurcus* Barbour 1921, *sensu* Becker et al 2019) (circle) studied by Cabezas-Cartes et al. (2014), (**c**) Photograph taken 6 months after the eruption of Puyehue-Cordón Caulle volcanic complex in the type locality of *P. spectabilis* (= *P. spurcus*)

Liolaemus lemniscatus and *L. pictus* from Chile, which seem to cope well with ash produced by volcanoes or fire. After ash deposition, lizards were able to emerge from their burrows, search for and feed on insects by following their tracks in the ash, suggesting starvation might not be the main source of immediate mortality after a disturbance (Mora and Labra 2017). In general, arthropod abundance decreased with volcanic disturbance, but the short-term effects of Cordón Caulle volcano ash on arthropod populations were according to ash grain shape, size, deposit thickness, and density in the air (Fernández-Arhex et al. 2013; Elizalde 2014). Effects were subtle on some groups like beetle assemblages protected by tree canopy in mountain forests (Ruggiero and Werenkraut 2014). Moreover, some lizard species may have been favored with the environmental changes produced by ashfall such as *Phymaturus sinervoi* that attained higher maximum sprint speeds over ash than over other substrates (Ibargüengoytía et al. 2016, probably related to their ancestral psammophilous habits; unpublished data).

13.3 Climate Change Effects on Lizards' Populations

Climate change has been noticeable in Argentina with greater temperature extremes, heat waves, and a remarkable reduction in precipitation in the Andes mountains and across most of Patagonia (Barros et al. 2014). In terms of temperature, Patagonia can be defined as a temperate or cold temperate region (Paruelo et al. 1998). Mean annual temperature ranges from 12 °C in the northeast to 3 °C in the south. However, toward the southwest, absolute minimum temperatures can reach values lower than −20 °C. In Patagonia, mean annual daily thermal amplitude varies with latitude (16 °C in north-central Río Negro Province and 5 °C in the southern extreme of Patagonia, Paruelo et al. 1998; Chap. 4). The Representative Concentration Pathway (8.5 scenario, IPCC 2014) for the next 50 years for this area estimates increases of 3.5–4 °C in annual means with the greatest change occurring in summer (Barros et al. 2014). In addition, the incremental warming rate is expected to be about five times greater than that experienced during the twentieth century (Meehl et al. 2007).

Patagonia shows a dramatic transition of environments and climate from the Andes to the Atlantic coast. The combined effects of seasonal movement, of the low- and high-pressure systems, and the ocean currents moving to an equatorial direction result in strong and prevailing westerly winds. The influence of the Pacific air masses and the topographic barrier of the Andes, parallel to the Pacific coast, results in a strong west–east gradient of precipitation (Barros et al. 1979, 2014). Most of the precipitation is discharged in the coastal mountains of Chile and on western slopes of the Andes, and the air warms and dries as it descends on the Argentine side of the Andes, an area whose mean annual rainfall ranges from 1200 mm in the northwest to 100 mm in the desert plains of southeastern Patagonia (Barros et al. 2014). The climatic trend observed during the last century, characterized by an increment in precipitation in northern Argentina and a reduction in the southwest, will be accelerated with a reduction in winter precipitation in response to increased greenhouse gas concentrations (RCP 4.5 and 8.5 scenarios, Intergovernmental Panel on Climate Change – IPCC 2014; Alexander et al. 2013; Barros et al. 2014).

Recent climate change projections led biologists to classify the threat to biodiversity at high altitudes in the Andes as severely threatened, because of the reduction in water availability due to receding glaciers, land degradation, and desertification (IPCC 2014; Barros et al. 2014). The alteration of fire regimes in the forest and steppe has an aggravated impact on the biota. In Patagonia, between 1999 and 2005, 2.7 M ha burned in 17,000 fires, with 85% of the surface affected and 82% of the fires concentrated in Río Negro province (de Torres Curth et al. 2008). Thus, the changes that are possible within accepted scenarios for Patagonia could be critical for lizard populations by directly or indirectly affecting their opportunities to move to refuges (Robinson et al. 2013), reproduce, and forage (Sinervo et al. 2010; Kearney 2013), resulting in the extirpation of some local populations (Kubisch et al. 2016a) and retractions of others (Vicenzi et al. 2017).

Nevertheless, the impact of climate change on lizards depends on extrinsic abiotic factors like temperature, thermal amplitude, precipitation, and biotic factors like predators, competitive interaction with invasive species (Mack et al. 2000), an influx of pathogens (Lafferty 2009), changes in vegetation, and food availability (Gilbert and Miler 2016). Among intrinsic factors, the physiological sensitivity and plasticity and the efficiency in thermoregulation can mitigate the impacts of climate change (Williams et al. 2008; Deutsch et al. 2008; Piantoni et al. 2016). In fact, if adaptive responses are slow relative to global warming, then changes in habitat suitability and increases in fragmentation will isolate populations and increase their vulnerability in the coming decades (Chevin et al. 2010; Huey et al. 2010; Sinervo et al. 2010; Pincheira-Donoso et al. 2013).

The general tendency shows that species are changing their distribution toward higher latitudes or altitudes (Chen et al. 2011). The cold temperate environment represents a potential thermal refuge for many lizard populations that live in warmer environments at lower latitudes and altitudes (Cabezas-Cartes et al. 2019; Piantoni et al. 2016). In northern Patagonia, *Liolaemus elongatus*, mostly known from steppe environments (Cei 1986), was observed in 1998 for the first time in the transition forest in sympatry with *L. pictus* (Ibargüengoytía and Cussac 1998), and in 2018 it was first seen at 2050 m a.s.l. in sympatry with *L. lineomaculatus* (Ibargüengoytía, unpublished data).

13.4 Immune State: Effects on Thermal Biology and Running Performance

Rapid shifts in geographic range when seeking for cooler environments may result in threats in the form of new competitors and pathogens (Cahill et al. 2012). In addition, in temperate environments, shorter and milder winters would trigger an increase in the spread of new diseases (Harvell et al. 2002). Nevertheless, the resilience of lizard populations to novel host–pathogen interactions will be governed by the interplay of immune state and the behavioral and physiological plasticity to adjust to the new challenges (Graham et al. 2011). Traits such as thermoregulation and running performance are usually linked directly to ecophysiological adaptation and can be affected by pathogens exerting selection pressures on their hosts (Graham

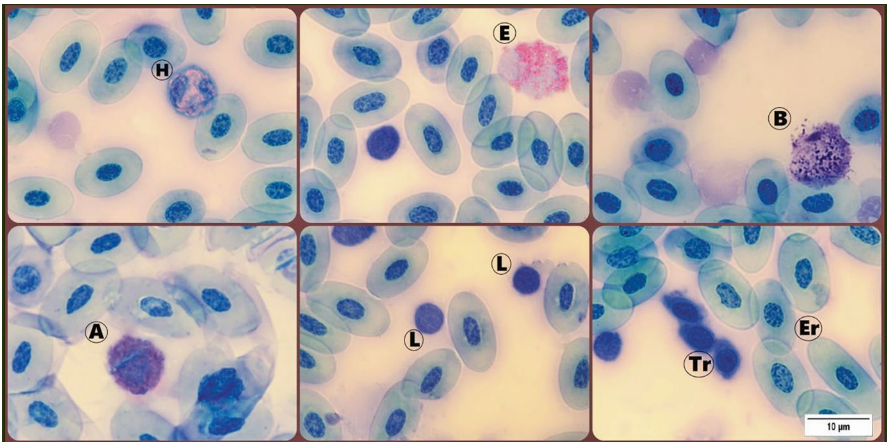

Fig. 13.2 Selected photographs of the blood cells found in *Liolaemus sarmientoi*. Leukocytes: heterophil (H), eosinophil (E), basophil (B), azurophil (A), and lymphocytes (L) erythrocytes (Er) and thrombocytes (Tr). May-Grünwald Giemsa stain. Bars = 10 µm

et al. 2011; Zamora-Camacho et al. 2014). Lizards can balance the benefit of an immune response and the cost of thermoregulation (a consequence of the effect of higher body temperatures of free-ranging lizards (T_b) on metabolic rate). This trade-off leads populations to exhibit high variability in the magnitude and efficiency of immune responses (Schmid-Hempel 2011).

In the same way, recent studies show that thermoregulation and locomotor performance of individuals of *L. sarmientoi* varied according to the leukocyte profile, suggesting a physiological adjustment to enhance the immunological response to infection, disease, or stress (Duran et al. 2019). Lizards selected high temperatures in thermal gradients in laboratory free from restriction related with temperature, predators, or social interactions (T_{pref}, sensu Hertz et al. 1993) while showing a high percentage of some leukocytes like eosinophils and basophils or a low percentage of monocytes (Fig. 13.2). In addition, Duran (unpublished data) found that individuals of *Liolaemus kingii* injected with LPS (lipopolysaccharide of the cell wall of *Escherichia coli*, treatment) thermoregulated accurately and at stable temperatures within T_{set} (interquartile of T_{pref}). Conversely, lizards injected with phosphate-buffered saline (PBS, control) showed a variable and lower T_{pref} (Fig. 13.3). These preliminary studies performed on *L. sarmientoi* and *L. kingii* suggest that lizards experiencing an immune response maintain temperatures higher than T_{pref} or within T_{set} and more stable than healthy lizards, probably to improve phagocytic activity by thermoregulation, a widespread mechanism in vertebrates (Zimmerman et al. 2010).

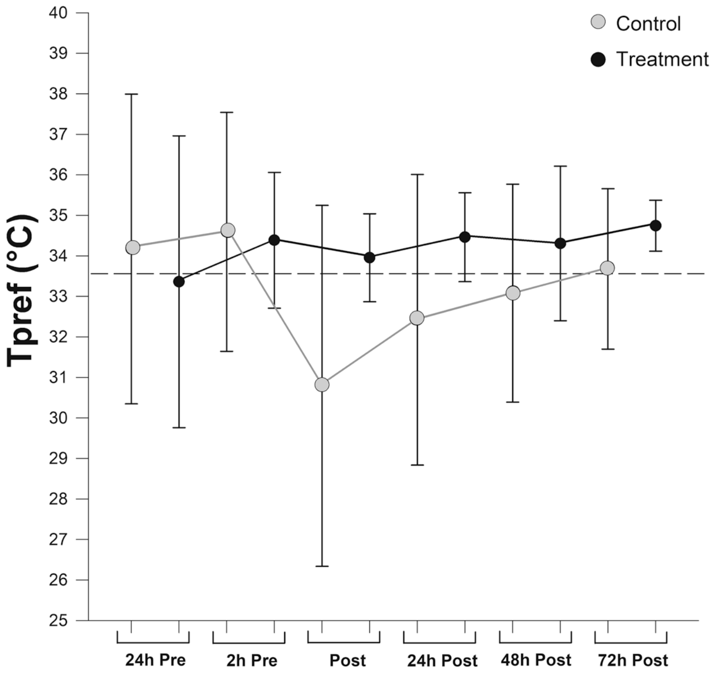

Fig. 13.3 Effects of injection on thermoregulation (T_{pref}) of two groups of adult male of *Liolaemus kingii*, from 24 h before and 72 h after injection. A group injected intraperitoneally with a saline solution as control group (PBS), free of antigens ($N = 10$, gray dots and lines), and another group injected with lipopolysaccharide of the cell wall (LPS, 2.5 μg endotoxin/g body mass), as treatment group ($N = 10$, black dots and lines). Means ± standard errors are indicated. Dashed lines indicate the mean preferred body temperature (T_{pref})

13.5 Environmental Restriction for Effectiveness of Thermoregulation

Temperature is particularly relevant because of its vital role over the biochemical and physiological functions, which affect the organism at all levels, from the rate of biochemical reactions at cellular level to whole organism physiological processes (Tattersall et al. 2012). Thus, most of physiological functions are thermally sensitive including digestion (Angilletta Jr et al. 2002), respiration (Al-Sadoon 1986, 1987), circulation (de Vera Porcell and Gonzalez 1986), locomotion (Bauwens et al. 1995), feeding (Van Damme et al. 1991), growth (Sinervo 1990; Kubisch et al. 2012; Gutiérrez et al. 2013), development (Castilla and Swallow 1996), and, hence, social behavior and reproduction (Sinervo et al. 2010; Tattersall et al. 2012). Knowledge of the body temperatures of free-ranging lizards (T_b), the preferred body temperatures using thermal gradients in laboratory (T_{pref}), and the effect of immunological states on lizard T_b-values allow us to infer how they will cope with predicted environmental changes (Paranjpe et al. 2014).

The ability of most lizards to control T_b within relatively narrow ranges through behavioral thermoregulation (De Witt 1967; Huey et al. 2003; Bartholomew 2005; Kearney et al. 2009) allows them to partially avoid or buffer increased temperatures (Kearney et al. 2009; Clusella-Trullas and Chown 2011). In this regard, it is necessary to know the operative environmental temperatures that represent the availability of thermal microenvironments for thermoregulation (T_e, Porter et al. 1973; Bakken 1992), also defined as the T_b that a non-thermoregulating lizard might experience in their natural environment (Hertz 1992). These parameters allow the calculation of the deviation of T_b of an individual from the set point range ($d_b = \sum|T_b - T_{set}|$), the mean thermal quality of a habitat from an organism's perspective ($d_e = \sum|T_e - T_{set}|$), and the effectiveness of thermoregulation in a given habitat [$E = 1 -$ (Mean d_b/Mean d_e); sensu Hertz et al. 1993]. Thus, the effectiveness of thermoregulation (E) will depend not only on the behavioral and intrinsic characteristics of the individuals but also on the heterogeneity of the thermal environments (Medina et al. 2009; Gutiérrez et al. 2010; Clusella-Trullas et al. 2011; Piantoni et al. 2016; Duran et al. 2018). Furthermore, there is a complex interplay among ecological and physiological traits that imposes limitations on thermoregulation and on the geographic distribution of the species, such as food availability, competition (Labra 1995), nesting sites, and predator abundance (Huey 1982), together with the reproductive (Medina et al. 2011) and immunological demands of the lizards (Tracy and Christian 1986).

Intraspecific comparative studies of thermal biology of *Liolaemus* populations from different latitudes and elevations (Medina et al. 2009, 2011) show that some species from the steppe maintain similar body temperatures and a common pattern of low variability in their effectiveness of thermoregulation by using different thermal microenvironments (Medina et al. 2009; Ibargüengoytía et al. 2010; Medina et al. 2011; Piantoni et al. 2016; Fig. 13.4; Table 13.1). For example, a study at two locations of three sympatric species, *Liolaemus bibronii*, *L. boulengeri*, and the viviparous *L. lineomaculatus* (Esquel 43° S 70′ W at 1400 m a.s.l.; Perito Moreno 46° S 71° W 263 m a.s.l.), shows that they compensate for the differences in the substrate and air temperatures and during cold windy conditions, they use different heat sources and exhibit differing activity timetables (Medina et al. 2011). *Liolaemus boulengeri* and *L. bibronii*, even when they are syntopic, choose different microenvironments that offer diverse challenges impelling lizards to find different behaviors for heat gain, and the populations at lower latitude of *L. bibronii*, *L. boulengeri*, and *L. lineomaculatus* are mainly heliothermic, while at higher latitude, the same species acquire heat by thigmothermy. Maintenance of similar T_bs at different latitudes suggest that lizards from colder environments at high latitude spend more time finding appropriate microenvironments for thermoregulation in detriment to other activities such as feeding and reproduction, and consequently they could be more exposed to predators (Pianka and Pianka 1970; Avery 1976; Huey and Slatkin 1976; Hertz and Huey 1981). In the same way, the southernmost lizards of the world (50–52° S), the psamophilous *L. magellanicus* and the saxicolous *L. sarmientoi*, show opportunistic thermoregulatory behavior and behave as heliotherms when air temperature is cold during the morning but gain heat from the substrates

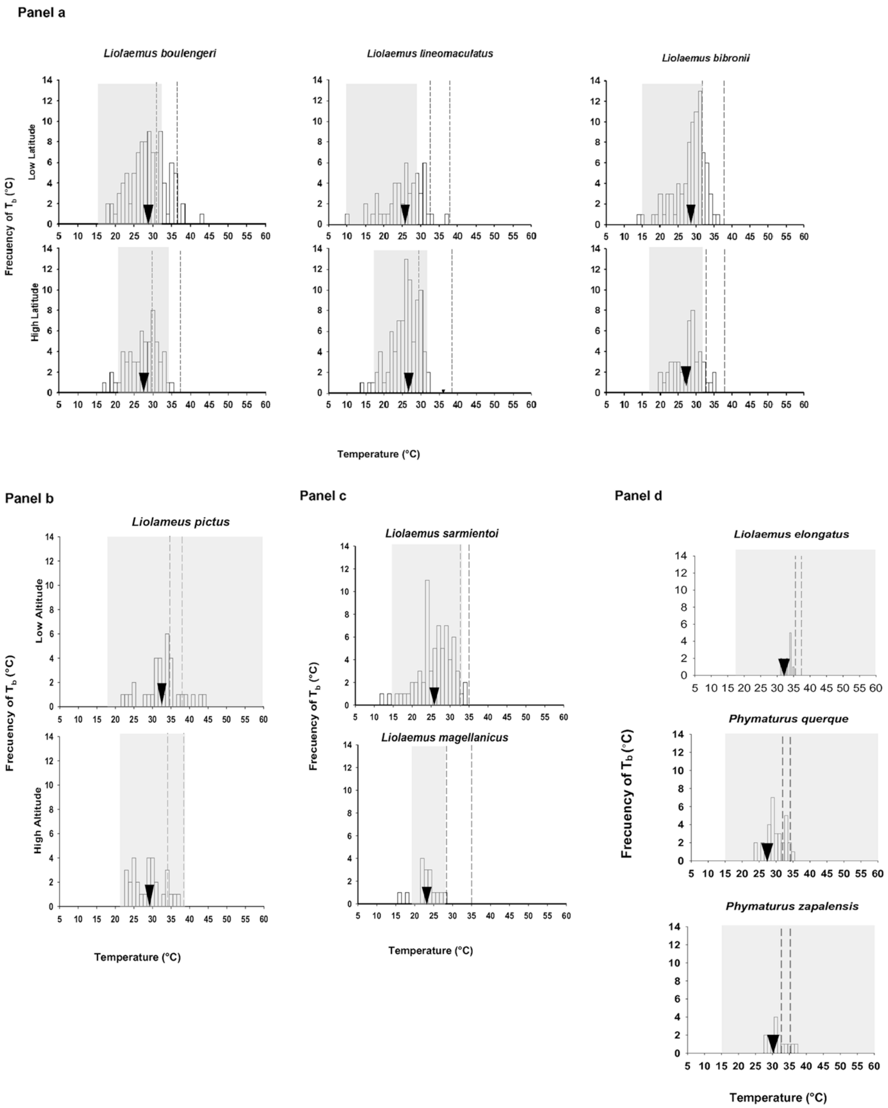

Fig. 13.4 (Panel **a**) Distribution of body temperature (T_b) of *Liolaemus boulengeri*, *L. lineomaculatus*, and *L. bibronii* at low (upper graphs) and high latitude (lower graphs) in Esquel and Perito Moreno, respectively; studied by Medina et al. (2011). (Panel **b**) Distribution of body temperature (T_b) of *L. pictus argentinus* at 771 m a.s.l. (Melipal Beach, Lake Nahuel Huapi, upper graph) and at 1615–1769 m a.s.l. (Chalhuaco Mountain, lower graph); studied by Gutiérrez et al. (2010). (Panel **c**) Distribution of body temperature (T_b) of *L. sarmientoi* (upper graph) and *L. magellanicus* (lower graph); studied by Ibargüengoytía et al. (2010). (Panel **d**) Distribution of body temperature (T_b) of *L. elongatus*, *Phymaturus querque* and *P. zapalensis* from 39° S latitude and 824–1312 m a.s.l.; studied by Duran et al. (2018). The gray area indicates range of operative temperatures (T_e) at capture; the dashed lines indicate the lower and upper set points of the preferred body temperature (T_{set}), and the black triangles indicate the mean T_b

Table 13.1 Descriptive data of individual deviation of T_b from T_{set} (d_b), the index of the average thermal quality of a habitat from an organism's perspective (d_e), and the effectiveness of temperature regulation (E), for *Liolaemus* and *Phymaturus* of Patagonia

	d_b	d_e	E
Liolaemus bibronii			
Low latitude (43°S 70°W, 626 m a.s.l.)	4.7 ± 0.7 (46)	8.42	0.44
High latitude (46°S 71°W, 263 m a.s.l.)	5.9 ± 0.7 (47)	10.87	0.45
Liolaemus boulengeri			
Low latitude (43°S 70°W, 626 m a.s.l.)	3.3 ± 0.5 (44)	8.2	0.59
High latitude (46°S 71°W, 263 m a.s.l.)	3.1 ± 0.5 (46)	6.2	0.5
Liolaemus lineomaculatus			
Low latitude (42°S 71°W, 1400 m a.s.l.)	6.9 ± 0.8 (53)	12.6	0.45
High latitude (46°S 71°W, 263 m a.s.l.)	4.5 ± 0.4 (73)	7.7	0.41
Liolaemus pictus argentinus			
Low altitude (41°S 71°W, 771 m a.s.l.)	5.6 ± 0.8 (27)	9.47	−0.24
High altitude (41°S 71°W, 1700 m a.s.l.)	6.5 ± 1.0 (30)	5.20	0.4
Liolaemus sarmientoi			
50°S 72°W, 980 m a.s.l.	6.8 ± 0.6 (53)	9.9 ± 0.5	0.30
Liolaemus magellanicus			
51°S 70°W, 133 m a.s.l.	5.4 ± 1.3 (36)	5.15 ± 1.85	−0.04
Liolaemus elongatus			
39°S 70°W, 824–1312 m a.s.l.	2.29 ± 0.51 (10)	6.95 ± 1.45	0.67
Phymaturus querque			
39°S 70°W, 824–1312 m a.s.l.	4.97 ± 0.50 (32)	8.89 ± 0.70	0.44
Phymaturus zapalensis			
39°S 70°W, 824–1312 m a.s.l.	3.28 ± 0.70 (14)	6.21 ± 1.12	0.47

Mean ± standard error and sample size (N)

(thigmothermy) during the early afternoon, when rocks and soil have warmed up (Ibargüengoytía et al. 2010).

Another comparative study yielded different results. Observation of two populations of *L. p. argentinus* at different elevations (771 and 1700 m a.s.l.) in northwestern Patagonia, Argentina (41° S 71° W), shows that both environments impose strong effects on the efficiency of thermoregulation displayed by lizards. *Liolaemus pictus argentinus* is a viviparous and insectivorous species with a wide distribution in the Patagonian Andes of Neuquén, Río Negro, and Chubut provinces of Argentina (39–43° S and 520–1600 m a.s.l., Cei 1986; Scolaro 2005). The high-elevation population inhabits the shady understory of a closed forest dominated by *Austrocedrus* and *Nothofagus* near the summit of Chalhuaco Mountain and attains only a low mean T_b (29 °C). At the low-altitude site, *L. p. argentinus* lives by the lakeshore in a rocky microenvironment with greater exposure to sunlight. These lizards attain a higher T_b (33 °C) probably because they can bask and be active during longer periods taking advantage of thermal inertia of the rocky substrate (Gutiérrez et al. 2010). In the high-altitude environment, the forest challenges thermoregulatory ability (high d_e), and lizards behave as moderate efficient thermoregulators ($E = 0.4$). Meanwhile, lizards in the low-latitude site showed an E-value of −0.24, suggesting that even microenvironments available in the range of their T_{set} are not selected. This anomaly likely occurs because of non-energetic factors such as disturbances by people on the public beach, predators hunting for lizards basking in the open, or concentrations of food in habitat patches otherwise unsuitable for thermoregulation.

The capacity to reach and maintain body temperatures within a range that allows activity and optimizes physiological performance depends not only on the availability of suitable microhabitats for thermoregulation but also on the spatial arrangement of the thermal resources (Sears et al. 2016). *Phymaturus* lizards are robust rock dwellers with flattened bodies that can shelter in small rock crevices where they spend most of their time (Cei 1986, 1993). *Phymaturus* are conservative in many aspects of their biology, being predominantly herbivorous, viviparous, and saxicolous (Cei 1986, 1993; Espinoza et al. 2004; Ibargüengoytía 2005; O'Grady et al. 2005; Boretto and Ibargüengoytía 2006, 2009). In the same way, it has been demonstrated that the thermal biology of *Phymaturus* is remarkably similar across a wide geographic range suggesting that it may be evolutionarily or ecologically constrained (Ibargüengoytía et al. 2008; Cruz et al. 2009) probably because of their low vagility and the similarity in their habitat (Debandi et al. 2012). In this regard, a comparative study of two sympatric species showed that *Phymaturus querque* ($E = 0.44$) and *P. zapalensis* ($E = 0.47$) behave as moderately efficient thermoregulators and specialists using narrow and deep cracks in the rocks as shelters. It is noteworthy that the two syntopic species selected thermal microenvironments colder than their T_{pref} during summer although warm microenvironments were available, probably to avoid overheating (Duran et al. 2018; Fig. 13.4, panel C). On the other hand, a population of *Phymaturus tenebrosus* from southwestern Río Negro behaves as a poor thermoregulator presenting the lowest E of all *Phymaturus* ($E = 0.19$) and also present operative temperatures lower than their optimal temperatures for locomotion (Cabezas-Cartes et al. 2019). As a result, the rising temperatures related to global climate change would favor the thermal physiology and locomotor performance of this species, possibly favoring its survival to global warming (Cabezas-Cartes et al. 2019).

Thermoregulatory behavior typically increases with latitude and altitude (except for the two southernmost liolaemids, *L. sarmientoi* and *L. magellanicus*, at 51° S) and that tropical and lowland lizards generally behave as thermoconformers (e.g., genera *Anolis* and *Tropidurus*; Piantoni et al. 2016), suggesting that species from lower latitudes and altitudes are more vulnerable to warming than temperate climate species (Huey et al. 2009; Piantoni et al. 2016). In tropical environments, the large proportions of individuals with T_b and T_e that exceed the population's T_{set}, together with the thermoconformity or poor thermoregulatory capacities, represent a risk of overheating and could restrict the hours of activity (Sinervo et al. 2010; Medina et al. 2016). In contrast with the tropics, lizards from Patagonia are characterized by having T_{pref} values much higher than the T_b and T_e, pointing out that in temperate environments, lizards face a greater challenge to raise body temperatures (Fuentes and Jaksic 1979; Medina et al. 2009, 2011; Ibargüengoytía et al. 2010; Piantoni et al. 2016; Cabezas-Cartes et al. 2019). Thus, it is expected that temperate-zone populations may experience improved thermal conditions during global warming by having more thermoregulatory opportunities to improve their physiological performance (Ibargüengoytía et al. 2010; Fernández et al. 2011, 2017; Duran et al. 2019, also see Paranjpe et al. 2014; Cabezas-Cartes et al. 2019).

13.6 Prediction of Population Extirpations and Changes in the Distribution Ranges Due to Global Warming

The high and conservative T_{pref} observed in most liolaemids (Labra 1998; Ibargüengoytía 2005; Rodriguez-Serrano et al. 2009; Ibargüengoytía et al. 2010; Moreno-Azócar et al. 2013; Medina et al. 2012) suggest that warming could be neutral or beneficial to many populations (Piantoni et al. 2016). Nevertheless, local extirpations of liolaemids have been already observed from 1975 to 2010, including at least three populations in South America. Affected species include *Liolaemus lutzae*, *L. fittkaui*, and *Phymaturus tenebrosus* (Sinervo et al. 2010). Sinervo et al. (2010) showed that one of the main mechanisms that could drive lizard populations to extinction is the increase in the hours of restriction (H_{r}), considered to be the daily time span lizards stay sheltered due to temperatures exceeding their thermal preferences (Sinervo et al. 2010; Kubisch et al. 2016a; Vicenzi et al. 2017). The physiological limit to which a species is adapted is reflected by the most extreme hours of restriction observed across the species range (e.g., at the warm temperature limit) during the breeding season. When the local hours of restriction climb above this value, local extinction and extirpation is predicted because the retreat into cooler shelters has detrimental effects on sociality, feeding, and reproduction (Sinervo et al. 2010).

For lizards of Patagonia, Kubisch et al. (2016a) estimated the current and future H_{r} under a global warming scenario for three species and predicted the proportion of populations to be extirpated by 2080 as 20% in the nocturnal gecko *Homonota darwinii*, 15% in *L. pictus*, and 26% in *L. elongatus*. In addition, a species distribution model performed for 14 Patagonian species, corresponding to three *Liolaemus* clades, predicted that future range boundaries would shift toward higher altitudes and latitudes (Bonino et al. 2015). Most of these species (*L. coeruleus*, *L. petrophilus*, *L. kriegi*, *L. escarchadosi*, *L. hatcheri*, *L. lineomaculatus*, *L. sarmientoi*, and *L. baguali*) may suffer a decrease in the size of their geographic range and may be seriously affected. But four of these species (*L. fitzingerii*, *L. xanthoviridis*, *L. boulengeri*, and *L. elongatus*) may increase their range with suitable climatic conditions (Bonino et al. 2015). However, this increase of area and expansion of the species distribution is not ensured, mainly because of their limited dispersal ability and geographic barriers. Case in point, *Phymaturus palluma*, an endemic lizard from the Central Andes, is expected to experience reductions in the number of suitable microhabitats in its current range, and, although such microhabitats may increase in availability in areas to the south and west, they may not be able to get there because of an inhospitable habitat matrix in between (Vicenzi et al. 2017). Whether lizards can move toward more suitable habitat patches will depend on their vagility, plasticity in behavioral habitat selection, and the presence of habitat continuity or corridors (Buckley et al. 2013). For example, the high degree of morphological and physiological specialization of *Phymaturus* species that occupy isolated rock promontories in the steppe, the rapid environmental change rate as the product of global warming, and the fact that much of the intervening lands are modified for agriculture or ranching (Feeley and Silman 2010) prevent dispersion of these species to more suitable areas (e.g., *P. palluma*, Vicenzi et al. 2017).

13.7 Performance and Physiological Plasticity

The trade-offs among thermal biology, performance, and ecology are shaped by intrinsic factors (genetic and epigenetics) and extrinsic pressures imposed by biotic (predators, food resources, competition) and abiotic (temperature, relative humidity). This complex interplay will determine whether lizards need to maximize performance in one function over another trait in nature (Huey and Stevenson 1979), and this system can vary temporally (seasonally), geographically (latitude, elevation), during ontogeny, or according to reproductive demands (adult vs juvenile, pregnant vs nonpregnant, Fernández et al. 2017). Individuals can select optimal temperatures that maximize some physiological functions, in detriment of having suboptimal temperatures for other functions (Huey and Stevenson 1979).

The knowledge of optimal temperatures for running performance combined with the temperature that lizards experience in their environment (T_b) allows the inference of how close species are to their thermal limits in nature and is essential to predict potential responses to a changing climate (Huey and Kingsolver 1989, 1993; Tattersall et al. 2012). In ectotherms the speed of locomotion depends on several factors like morphology (Irschick et al. 2005; Kubisch et al. 2011), reproductive status (Sinervo et al. 1991; Kubisch et al. 2011), sex (Irschick et al. 2005), substrate (Tulli et al. 2012; Cabezas-Cartes et al. 2014), habitat use (Irschick et al. 2005), the time of the day (Ibargüengoytía et al. 2007), and immune state (Paranjpe et al. 2014; Duran et al. 2019), among others. The most influential variable affecting running performance is temperature (Angilletta Jr et al. 2002; Tattersall et al. 2012). Thermal performance curves (Huey and Stevenson 1979) extend within the thermal critical minimum (CT_{min}) and the thermal critical maximum (CT_{max}) limits (i.e., where performance equals zero). From CT_{min}, lizards' locomotor performance increases and reaches a peak (i.e., maximum speed) at the optimal body temperature (T_o), and then decreases rapidly as temperature approaches CT_{max} (Huey and Stevenson 1979; Hertz et al. 1983; Huey and Bennett 1987; Angilletta Jr et al. 2002). The performance breadth corresponds to the range of temperatures over which an animal performs at a selected proportion of their maximal performance (e.g., 80% or 95%, Angilletta Jr et al. 2002; Tattersall et al. 2012; Huey et al. 2012). In the austral *Liolaemus*, the T_o for running performance is higher than the body temperature they can achieve in their natural environments (Bonino et al. 2011; Fernández et al. 2011; Fig. 13.5). Displacement to colder environments of these austral species in the past could have led to lower locomotor capacities, possibly mitigated only in part by subsequent adaptation (Fernández et al. 2011). Therefore, it is expected that an increase in temperature would favor performance of many lizard cold temperate populations (Fernández et al. 2011; Cabezas-Cartes et al. 2019).

For example, for the southernmost species, *L. sarmientoi*, and especially for *L. magellanicus*, there is a great difference between thermal optima for locomotor performance and body temperature that lizards can achieve by thermoregulation in nature (Fernández et al. 2011; Fig. 13.5d, e). These lizards presented the lowest body temperatures obtained for the genus *Liolaemus* (27 °C, Jaksic and Schwenk 1983; 23–26 °C, Ibargüengoytía et al. 2010), but the T_{pref} values obtained in the laboratory for both species (32–34 °C, Ibargüengoytía et al. 2010) were similar to those of congeners (Labra 1998; Medina et al. 2009). The same pattern was observed in the southernmost nocturnal gecko *Homonota darwinii* (Ibargüengoytía et al. 2007; Fig. 13.5a), the saxicolous *L. elongatus* (Kubisch et al., unpublished data; Fig. 13.5c), and *Phymaturus tenebrosus* (Cabezas-Cartes et al. 2019). However, in the north of Patagonia, *L. pictus argentinus* shows average body temperatures in the field higher than the T_o ($T_b = 32$ °C, $T_o = 26$ °C, Kubisch et al. 2016b). Thus, *L. pictus* seems to be the most vulnerable as its capacity to disperse, forage, and perform social activities is expected to be affected under an increment of environmental temperature (Kubisch et al. 2016b). In addition, the thermal safety margin (TSM) for physiological performance of *L. pictus* (T_o – mean T_e, sensu Deutsch et al. 2008; Logan et al. 2013) was 0.43 °C in long runs and 0.64 °C in sprint runs suggesting that the environmental temperatures are already close to the physiological optimal temperature in this species (Kubisch et al. 2016b). It is noteworthy that the TSM in *L. pictus* was lower than in four tropical species of *Anolis* (TSM ranging from 1.5 to 5.5 °C, Logan et al. 2013). Nevertheless, *L. pictus* can run at 80% or more of its $V_{\max}$ around a wide range of temperatures close to T_o ($B_{80} = 17$ °C, Fig. 13.6), and the warming tolerance (WT = mean $T_e - \mathrm{CT}_{\max}$, sensu Deutsch et al. 2008, Logan et al. 2013) is much higher than those found for four tropical *Anolis* species (WT = 3.1 – 7.8 °C, Logan et al. 2013). The high WT in *L. pictus* (WT = 17.71 °C, Kubisch et al. 2016b) shows that this species could attenuate the impact of global warming on performance even though they show a very low TSM (Fig. 13.6).

In addition, it is expected that lizards, when possible, select temperatures that maximize physiological performance (T_{pref} near the T_o). A review (Martin and Huey 2008) of 63 species from the northern hemisphere showed T_o is often above T_{pref}. In Patagonian lizards, the same was found in *L. elongatus* (Kubisch et al., unpublished data; Fig. 13.5c), *L. kolengh*, and *L. hatcheri* (Bonino et al. 2011). Nevertheless, other studies of lizards of Patagonia showed that their optimal temperatures for maximum locomotor performance are near or below the lowest T_{set}, as is the case for *Homonota darwinii* (Ibargüengoytía et al. 2007; Aguilar and Cruz 2010; Fig. 13.5a),

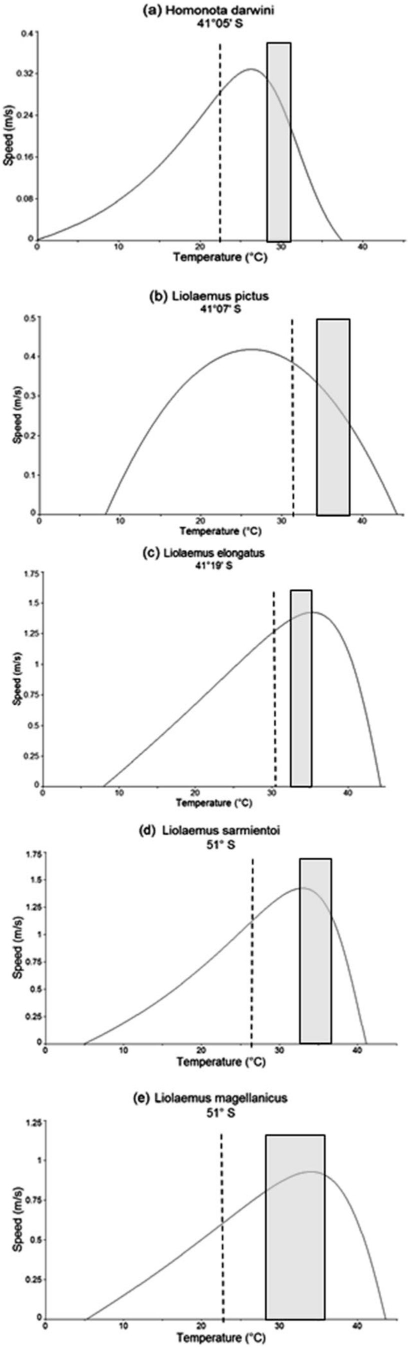

Fig. 13.5 Estimated performance curves of the relationship between speed and body temperature in five species of Patagonian lizards from northern to southern latitude: (**a**) *Homonota darwinii*, (**b**) *Liolaemus pictus*, (**c**) *L. elongatus*, (**d**) *L. sarmientoi*, and (**e**) *L. magellanicus*. Vertical dashed line indicates the mean field body temperature. The gray rectangle indicates the set point range of preferred temperatures

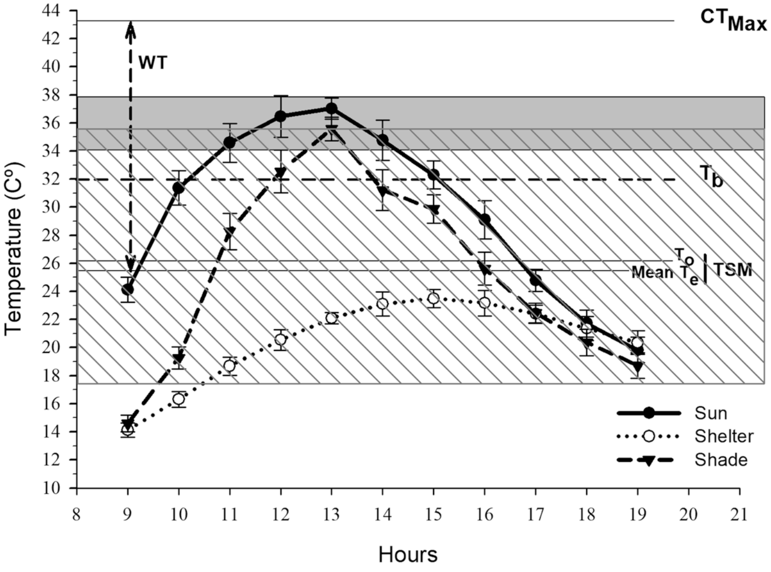

Fig. 13.6 Operative temperature (mean ± standard error) every hour during activity span, obtained from plastic models placed in different thermal microenvironments. The mean operative temperature (T_e), the critical thermal maximum (CT_{Max}), the mean body temperature in field (T_b), and the optimal performance temperature (T_o) of *Liolaemus pictus* are indicated with horizontal lines. The warming tolerance (WT) and the thermal safety margin for physiological performance (TSM) are indicated with arrows. The gray rectangle represents the set point range of the preferred body temperature in laboratory that corresponds to the 25 and 75% quartiles. The rectangle with diagonal stripes corresponds to the thermal performance breadth (B_{80} = range of body temperature over which the lizard can run at 80% or faster of its maximum speed)

L. sarmientoi (Fernández et al. 2011; Fernández, unpublished data; Fig. 13.5d), *Liolaemus pictus* (Kubisch et al. 2016b; Fig. 13.5b), *L. baguali*, *L. escachardosi*, *L. gallardoi*, *L. kingii*, *L. lineomaculatus*, and *L. zullyi* (Bonino et al. 2011). For the southernmost reptile, *Liolaemus magellanicus*, the T_o is included in their set point range of preferred temperatures (Fernández et al. 2011; Fernández, unpublished data; Fig. 13.5e) even though they are very unlikely to find in nature.

However, the thermal performance curve can vary as an individual acclimates to the temperature and time of exposure in a particular environment (Somero 2010; Tattersall et al. 2012), and this physiological plasticity allows ectotherms to exploit novel environments (Huey and Kingsolver 1989, 1993). The changes in the performance curves are considered acclimatization if they occur by natural changes in the environment, but they are called acclimation if they are consequence of manipulation in the laboratory (Huey et al. 2012). Acclimation capacity of thermal physiology in lizards (Paranjpe et al. 2013) can potentially ameliorate projected extinctions due to climate change by upward of 10% (Sinervo et al. 2018). The “beneficial acclimation assumption” postulates that physiological plasticity confers advantages to the organism and should elicit a change in the phenotype that improves performance in the new environment (Leroi et al. 1994).

Although physiological plasticity is expected to occur mainly in higher-latitude species because their environments have greater seasonal amplitude (Stillman 2003), several Patagonian lizards like *Liolaemus sarmientoi*, *L. pictus*, *L. elongatus*, and *Homonota darwinii* show low plasticity in their performance variables during acclimation (Aguilar and Cruz 2010; Fernández and Ibargüengoytía 2012; Kubisch 2013; Kubisch et al. 2016b). *Liolaemus pictus* and *L. elongatus* showed limited plasticity in some physiological variables like the T_{pref}, the panting threshold (T_{panting}; the body temperature at which the individual opens its mouth to lose heat by evaporation; Kubisch et al. 2011), and the critical minimum temperature ($\mathrm{CT}_{\mathrm{min}}$; the body temperature at which the individual is no longer able to right itself when placed on its back) when lizards were acclimated to low temperatures (21 °C in *L. p. argentinus* and 22 °C in *L. elongatus*) or high temperatures (31 °C in *L. p. argentinus* and 30 °C in *L. elongatus*, Kubisch 2013; Kubisch et al. 2016b). The only case of plasticity reported for *Liolaemus*, which involves *L. pictus pictus* from Chile (Artacho et al. 2017), found plastic responses in T_{pref} among three populations acclimated at different temperatures.

Regarding running speed, Aguilar and Cruz (2010) also suggest a low acclimation capacity in *Homonota darwinii*, since they did not find maximum speed differences among groups acclimated to temperatures ranging from 18 to 33 °C. In *L. sarmientoi*, acclimation to a higher temperature (21 °C, higher than their mean natural environmental temperature during their activity period) resulted in a decrease in running speed (Fernández and Ibargüengoytía 2012), while in *L. pictus* and *L. elongatus*, the different acclimation temperatures (21 °C and 31 °C for *L. pictus* and 22 °C and 30 °C for *L. elongatus*) did not affect locomotor performance (Kubisch 2013; Kubisch et al. 2016b). The same pattern of limited acclimation plasticity exhibited by *H. darwinii*, *L. sarmientoi*, *L. pictus*, and *L. elongatus* was observed in the desert night lizard (*Xantusia vigilis*) to either 20 °C or 30 °C (Kaufmann and Bennett 1989), and this phenomenon has been seen in amphibians after metamorphosis (Wilson and Franklin 2000; Marvin 2003). Therefore, organisms experiencing a rapid increase in environmental temperature due to climate change may not be significantly plastic in their ability to behaviorally compensate their locomotor performance, which could influence directly their ability to escape from predators, forage, or do social activities. But *L. elongatus* showed partial acclimation in long runs, since the test group acclimated at 30 °C ran faster than that acclimated to 22 °C when run at 40 °C (Kubisch 2013). This result is congruent with the “beneficial acclimation assumption.” In this way, *L. elongatus* could dampen the effects of global warming in long runs.

13.8 Embryo Survivorship and Newborn Fitness

Environmental temperature also exerts a powerful effect on physiology during the embryonic development in reptiles. Reptile phenotypes are thus significantly plastic, and therefore they are a good biological model for the study of environmental effects on their life history strategies (Adolph and Porter 1993; Shine 1995; Elphick and Shine 1998; Shine and Elphick 2001; Lourdais et al. 2004; Cadby et al. 2014). Constraints on time of activity during the breeding season may affect the reproductive output and cause local extinctions (Sinervo et al. 2010, 2011; Kubisch et al. 2016a; Vicenzi et al. 2017). This mechanism occurs because embryos and juvenile lizards are particularly vulnerable to both acute and chronic disturbances at high temperatures, since they have lower thermal tolerance ranges than adults and lower thermal inertia (Buckley and Huey 2016). A chronic increase of temperature in early stages of ontogeny can influence the locomotor performance and behavior patterns that persist over time, affecting the biological adaptation of the species (Aidam et al. 2013; Angilletta Jr et al. 2013; Buckley and Huey 2016). For this reason, in particular, Pincheira-Donoso et al. (2013) predict that viviparous *Liolaemus* that inhabit temperate cold climates of the Andes are the most prone to suffer extirpations or major extinctions in the next half century, because viviparity evolved in the genus in cold climate environments and is probably adaptively restricted to such environments.

However, as mentioned above, in the austral and viviparous species *L. sarmientoi* (from 51° S), the T_e and T_b were much lower than their T_{set}, but the T_o for both short and long runs was within their T_{set} (Fernández et al. 2011; Fernández, unpublished data; Fig. 13.5d). Furthermore, recent studies show that the T_{pref} for pregnant *L. sarmientoi* females provides an optimal environment for embryo development in this viviparous lizard (Fernández et al. 2017). The T_b values that pregnant females attain by thermoregulation in a thermal gradient (T_{pref}) enhances offspring traits related to fitness, such as shorter gestation period, locomotor performance, and body condition, in contrast with the temperatures they would be exposed to if oviparous. In females exposed to temperatures that simulated natural environments for a potential nest, it was observed that their reproductive success decreases drastically and they produced low-quality offspring (Fernández et al. 2017). Similar results were found for other species such as the phrynosomatid lizard *Sceloporus virgatus* (Qualls and Andrews 1999) and in the soft-shelled turtle *Pelodiscus sinensis* (Du and Ji 2003). In addition, pregnant females of *L. sarmientoi* thermoregulate differently than nonpregnant females and achieve higher and more stable body temperatures compared to environmental temperatures suggesting that they precisely thermoregulate to promote successful embryonic development (Fernández et al. 2017).

Pregnant females also reduce their risk of predation and optimize energy expenditure (Lin et al. 2008; Fernández personal observation). If the variability of the T_{pref} tends to be lower in pregnant than in nonpregnant females, the optimum temperature range for embryonic development is also narrow, avoiding potentially lethal limits for embryos (Webb et al. 2006). In this way, when females reach optimum thermal levels for development, they maximize the benefits with relatively low reproductive costs (Wang and Dillon 2014). These results point out that this austral species is not well adapted in relation to the running ability and offspring development (Fernández et al. 2017). These results, in contrast with predictions of Pincheira-Donoso et al. (2013), show that at least some populations of viviparous liolaemids could benefit from higher environmental temperatures and therefore bear a lower risk of local extinction (Fernández et al. 2011, 2017).

13.9 Effects of Climate Change on Growth Rates, Age at Sexual Maturity, and Longevity

It has been demonstrated that increased climatic temperature can affect several life history traits such as clutch size (Winkler et al. 2002), fecundity (Barbraud and Weimerskirch 2001; Sanz et al. 2003), growth rates, and survival (Bestion et al. 2015). However, global warming effects might be reduced or mitigated in species with shorter generation times that would allow faster adaptation. Accelerated rates of warming would curtail such adaptive change. In contrast, in species with long generation times like some Patagonian lizards, the rate of temperature change may be too fast for lizard populations to cope with. Indeed, the *Phymaturus* and *Liolaemus* species of Patagonia studied so far exhibit delayed sexual maturity (3–9 years, Gutiérrez et al. 2013; Cabezas-Cartes 2016) and long life spans (7–16 years, Gutiérrez et al. 2013; Cabezas-Cartes 2016). In addition, all these species have mean reproductive outputs that are among the lowest in lizards (Chap. 12). These life history traits yield long generation times, which limits the rate of evolutionary change in these species. As a result, populations of Patagonia would be less able to adapt to the rapid increase in temperature as a consequence of global warming and more likely to become extinct in a short- or medium term (Sinervo et al. 2010; Kubisch et al. 2012).

The lizards living in temperate climates have cyclic seasonal growth, with rapid growth during the period of activity and an arrest of growth during brumation (Boretto et al. 2018). This is recorded in the long bones of lizards as annual growth rings that appear as broad layers (fast growth), concentric, and adjacent to narrower layers (slow growth). Through the histological examination of these patterns (skeletochronology), it is possible to estimate the individual age, longevity, age at sexual maturity, and age-specific growth rate (Saint Girons et al. 1989; Castanet and Báez 1991; Piantoni et al. 2006; Gutiérrez et al. 2013; Boretto et al. 2015; Cabezas-Cartes et al. 2015; Chap. 12). Furthermore, when longevity and age at sexual maturity are analyzed together with other characteristics, like clutch size and reproductive cycles, it is possible to make inferences about fecundity and the evolution of life history tactics in cold and warm environments (Piantoni et al. 2006; Chap. 12).

Preserved museum specimens were analyzed using skeletochronology by Kubisch et al. (2012) in order to understand how increased environmental temperature may affect populations, comparing individual growth rates, longevity, age at sexual maturity, and reproductive output from specimens obtained in 1941 and 2010 from two sites, one warmer continental site and one cooler and more coastal. Their results suggest that, under a scenario of global warming, the nocturnal gecko *H. darwinii* would not exhibit a negative fitness response but would increase growth rates and reproductive output, as was shown by the difference between the 1941 and 2010 samples at both sites. The effects of climate change over this 69-year time frame are still negligible when compared with the present-day continental-to-coastal differences in temperature, that is, those related to the proximity to the Andes vs. the coastal location. However, the three populations reached adult size at a minimum age of 3 years, but the maximum life span at the warm site was up to 9 years in the 1941 sample but only 5 years in the 2010 sample (Kubisch et al. 2012). These results corroborate the findings of Bestion et al. (2015) showing that warmer climate can be detrimental for the survival of older individuals and that the annual survival of adults and yearlings was lower in warm-climate environments (Bestion et al. 2015).

13.10 Conclusions

The origin of the family Liolaemidae dates from ~62 Ma (Townsend et al. 2011) and has passed through climatic and geological events resulting in acute and chronic disturbances for this clade. For example, reconstruction of the Pleistocene versus Eocene temperature regimes indicates that the family Liolaemidae has experienced long-term mean temperatures 6 °C lower than and up to 14 °C greater than recent relative means (1960–1990, IPCC 2014). Nevertheless, they may experience a greater increasing temperature rate (up to 7 °C higher than average) in the next 80 years that could drive several populations to extinction. In particular, if we consider the slow-lane lifestyle of Patagonian lizards (Boretto et al. 2018), we expect them to have less opportunity to adapt to rapid environmental changes. In Patagonia the family Liolaemidae is represented by the genera *Phymaturus* and *Liolaemus* (Donoso-Barros 1966; Cei 1986; Pincheira-Donoso et al. 2008), and the most extensive radiation in the family occurred in the genus *Liolaemus*, most probably boosted by a series of episodes of Andean uplift during the last ~25 Ma (Pincheira-Donoso et al. 2015). The Andes became a barrier to atmospheric circulation, changing the patterns of precipitation and seasonal heating, and was the main cause of the global cooling trend observed since the Eocene (Gregory-Wodzicki 2000). Since the Andean uplift, there has been a succession of earthquakes, volcanic eruptions, and fires that have depleted several lizard populations with a resulting legacy of a great diversity of life history traits in Liolaemidae, *Phyllodactylidae*, and Leiosauridae.

The Patagonian steppe has been subjected to a variety of volcanic eruptions since the Miocene, 23.3 Ma (Giacosa and Heredia 2004; Giacosa et al. 2005), and volcanism continues at the present. In particular, the Puyehue-Cordón Caulle volcanic complex (with a 2.5 km diameter) has been active the last 11,500 years with several explosive pulses (Lara et al. 2004). Recent eruptions were registered in 1893, 1914, 1919, 1921–1922, and 1960 (Singer et al. 2008). Following the most recent eruption in 2011, we found evidence of ecophysiological adaptations to volcano ash in lizard populations of *Phymaturus* in steppe environments (Ibargüengoytía et al. 2016) in Argentina and also to fire ash in *Liolaemus pictus* and *L. lemniscatus* on the other side of the Andes in the Austral forests of Chile (Mora and Labra 2017).

The present review shows that lizard populations from Patagonia experience both acute catastrophic events such as ashfall and chronic events such as the gradual increase in ambient temperature due to global warming, without drastic changes in locomotor performance, thermoregulatory capacity, or growth dynamics. Some species, like *L. elongatus* and the southernmost lizards of the world, *L. sarmientoi* and *L. magellanicus*, could benefit to some extent from global warming as warmer temperatures would reduce their costs of thermoregulation, improve locomotion, and enhance immunological performance (Fernández and Ibargüengoytía 2012; Duran et al. 2019). In addition, an increase in environmental temperatures in cold environments would increase the availability of thermal microenvironments favoring pregnant *L. sarmientoi* females, in which higher and stable temperatures are necessary to ensure newborn fitness and survivorship (Fernández et al. 2017). Although increased temperatures may help pregnant females in some species and reduce the costs of thermoregulation in others, it may harm other life stages or phenological events.

Climate change can force lizards to refuge several additional hours each day, decreasing the amount of time available for reproductive activity, feeding, and social behaviors (Sinervo et al. 2010; Kubisch et al. 2016a; Vicenzi et al. 2017). Thus, shifts are expected in the geographic ranges of lizard populations under a global warming scenario (Bonino et al. 2015), but this is strongly dependent not only on their vagility and dispersal behavior but also the speed of adaptive changes in traits such as habitat and diet selection. The general question is whether such range shifts and adaptations would occur quickly enough to prevent the collapse of populations due to the energetic restrictions imposed by global change (Vicenzi et al. 2017). For example, it is expected that in Patagonia global warming would affect in particular the genus *Phymaturus*, because it is highly specialized to live in rock promontories in the steppe environments (Scolaro 2005, 2006), an herbivorous diet (Espinoza et al. 2004) and a slow pace-of-life reproductive schedule (Boretto et al. 2018). Extirpations of populations have been observed already in the genus *Phymaturus* (Sinervo et al. 2010). In *Liolaemus* and the gecko *Homonota darwinii*, studies predict 15–26% of the populations to become extinct by the year 2080 (Kubisch et al. 2016a), and most *Liolaemus* species studied may suffer range reductions (Bonino et al. 2015).

In Patagonia, consideration of the actual low operative temperatures T_e, compared to the T_b values that lizards attain by thermoregulation in the field, and the high T_{pref} characteristic of the Liolaemidae family, explains why the genus *Liolaemus* has experienced low rates of extinction and why such rates are predicted to continue through 2080 despite global warming, compared to 12 other families of heliothermic lizards (Sinervo et al. 2010). Meanwhile, species located at lower latitudes in northern Argentina and Chile, and in Brazil, are considered more vulnerable to global warming (Piantoni et al. 2016). However, the fact that the environments in Patagonia represent a potential refuge for northern species may constitute a challenge for current-day Patagonian populations in terms of new predators, competitors, and pathogens (Paranjpe et al. 2014; Duran et al. 2019). The biodiversity of Patagonia and the high Andean habitats could be severely threatened not only by receding glaciers but also by land degradation, the desertification aggravated by the alteration of fire regimes in the forest and the steppe, and rapid global climate change (IPCC 2014; Barros et al. 2014).

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Chapter 14
Conservation Concerns About the Southernmost Lizards of the World

Federico Pablo Kacoliris, Ignacio Minoli, Camila Kass, and Diego Omar Di Pietro

Abstract Lizard populations are globally in decline due to several human-related threats, and the Patagonia region is not an exception to this problem. With more than 160 species, Patagonian lizards encompass a high percentage of the lizard diversity from South America. Among them, at least one-third are currently listed with some IUCN Red List threat category. These species are affected by several threats, among which some of the most harmful ones are related to energy production, mining, and agriculture. Among threatened species, the six most endangered are *Liolaemus confusus*, *Liolaemus curis*, *Liolaemus cuyumhue*, *Liolaemus hermannunezi*, *Liolaemus rabinoi*, and *Phymaturus vociferator*. These species deserve special attention, thus the areas where these lizards occur should be protected. However, in order to protect a higher number of species in the wild, alternative approaches should be undertaken to prioritize conservation areas, considering other sources of information including local politics, opportunities, social context, land availability, degree of habitat disturbance, and lizard biodiversity, among others. In this challenging scenario, the conservation of Patagonian lizards will require not only committed people, but also further research, adaptive management, sustainable development, and even citizen activism to promote a change in governmental decisions.

F. P. Kacoliris (✉) · D. O. Di Pietro
Sección Herpetología, División Zoología de Vertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata - CONICET, Buenos Aires, Argentina
e-mail: kacoliris@fcnym.unlp.edu.ar; dipietro@fcnym.unlp.edu.ar

I. Minoli
Instituto Patagónico para el Estudio de los Ecosistemas Continentales – Consejo Nacional de Investigaciones Científicas y Técnicas (IPEEC – CONICET),
Puerto Madryn, Chubut, Argentina

C. Kass
Sección Herpetología, División Zoología de Vertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata - CONICET, Buenos Aires, Argentina

Universidad Nacional de Chilecito, CONICET. Instituto de Ambiente de Montaña y Regiones Áridas (IAMRA), La Rioja, Argentina
e-mail: ckass@undec.edu.ar

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14.1 Lizards on the Edge: Global Situation of Endangered Reptiles

One of the most severe environmental problems caused by humans is global loss of biodiversity (Barnosky et al. 2011). Approximately 200 vertebrate species have disappeared in the past 100 years. This represents an increase of at least two orders of magnitude in the extinction rate when compared to what was recorded during the prevailing two millions years (Ceballos et al. 2017). This current biological annihilation is considered to be the sixth massive disappearance of biota since the emergence of life on Earth, and evidence shows it is mainly caused by human-related threats (Dirzo et al. 2014; Brook et al. 2008).

At present time, a great number of land vertebrate populations are in decline (Pimm et al. 2001). Some extinctions occur so fast (an average of two vertebrates per year) that it is not possible to study the consequences of these events (Ceballos et al. 2017). However, when considering the key role these animals play in ecosystems and the complex networks they integrate, a direct effect on other organisms including humans is highly expected (Steffen et al. 2011). Researchers and practitioners, concerned on this problem, have been working on preventing the extinction of vertebrates worldwide with a historical higher focus on large mammals and some charismatic birds. On the other hand, this situation left amphibians and reptiles underrepresented in conservation planning even when they show a bigger extinction risk than other groups (Pawar et al. 2007). Fortunately, reptiles have received more attention during the last decade than in the past.

Nowadays, reptiles are recognized as environmental heralds (Gibbons and Stangel 1999). It is well known that they play a key role in ecosystems as predators, preys, or seed dispersers; they are useful bioindicators of environmental health and are also model organisms in ecological and evolutionary researches (Pianka 1973; Read 1998; Raxworthy et al. 2008). However, a combination of narrow distributional ranges and higher degree of specialization to live in specific habitats makes reptiles more susceptible to environmental changes and disturbances when compared to other vertebrates, being endemic species generally the most affected (Huey et al. 1983; Jensen 2008). Reptiles are facing several human-related threats, including habitat loss and degradation, invasive species, environmental pollution, emerging diseases, unsustainable habitat use, and climate change (Gibbons et al. 2000; Sinervo et al. 2010; Böhm et al. 2013). These threats, alone or in combination, are increasing extinction risks in reptiles worldwide, and the Patagonia region is not an exception to this problem.

Patagonia is considered an area of high endemism of vertebrates (Lamoreux et al. 2006), and reptiles represent an important component of the Patagonian fauna.

Among reptiles, the Patagonian lizards show not only an incredible diversity of species but also a high number of endemisms (Chebez et al. 2005). This region is considered a "hot" center of origin and diversification source for some lizard genera, such as *Pristidactylus* Fitzinger (Lamborot and Diaz 1987; Scolaro et al. 2003), *Leiosaurus* Duméril and Bibron, *Diplolaemus* Bell (Cei et al. 2003), and *Phymaturus* Gravenhorst (Díaz Gómez 2009). Although several conservation projects are currently being carried out in Patagonia, lizards' hazards and problems are still not being fully addressed.

The current scenario of Patagonia with an increase in frequency and magnitude of threats coupled with the absence of sustainable policies makes the lizards' situation very worrying. In this chapter, we will summarize the current information related to conservation of Patagonian lizards. We will assess lizard biodiversity and conservation status, threats, priority species, and areas while evaluating management needs in order to promote conservation actions in a preliminary way. We hope this work serves as a baseline to promote the protection of lizards in this remote and pristine region from South America.

14.2 Diversity and Conservation Status of Patagonian Lizards

Geographic aspects of reptile diversification in arid environments (Pianka 1986; Melville et al. 2006) are represented in Patagonia with the second most diverse lizard genus, *Liolaemus* (Pincheira-Donoso and Scolaro 2007; Uetz 2018). This region is considered by several specialists a vulnerable, outstanding area at the regional level and with the highest regional priority for conservation (Dinerstein et al. 1995). Moreover, the Patagonian steppe has been included in the "Global 200" priority ecoregions for conserving the most outstanding and representative habitats for biodiversity on the planet (Olson and Dinerstein 2002). The contribution of Patagonian lizards to the Neotropical diversity, and therefore, to the importance of this area in the international context, is not negligible at all.

With a total of 169 described species (this number can show small differences depending on different taxonomic approaches), grouped within 12 genera, the richness of Patagonian lizards encompasses approximately 8% of the whole diversity of lizards described for the Neotropics (2086 described species, Uetz 2018). More than one-third of these Patagonian species are currently listed within some threat category at national and/or international Red Lists (Table 14.1). From the rest, at least 10% was not yet assessed, another 5% is categorized as data-deficient, and one species is listed as near threatened. Considering that several of these species have small distributional ranges and live in threatened habitats, we assume a great number of them will fall within a threat category after a deep assessment. These results mean that the current number of threatened lizard species living in Patagonia could reach

Table 14.1 Number of Patagonian lizards' species listed at each category in national and international Red Lists

	National Red List	IUCN Red List
Not assessed	24	22
Data-deficient	13	12
Least concern	78	120
Near threatened	1	1
Vulnerable	42	5
Endangered	6	6
Critically endangered	5	3

approximately 50%; a number that will probably increase in the short term if the current trends of human-related threats continue.

A high number of lizard species from Patagonia are endemic to the region. Among them, the higher number of endemics belongs to the diverse family Liolaemidae, with almost all of its species included within the genera *Liolaemus* and *Phymaturus*. *Liolaemus* is the second most diverse genus of Iguania, and the Patagonia region harbors approximately 40% (112 species) of the total species richness within this clade (Pincheira-Donoso and Scolaro 2007; Abdala and Quinteros 2014). Among these species, approximately 30 are endemic to Patagonia (Corbalán et al. 2011), and 10 of them are listed in some threat category at the IUCN Red List, meaning that 26% of threatened *Liolaemus* live in this remote region.

The genus *Phymaturus* is mainly endemic from Patagonia with part of it living in neighboring regions. *Phymaturus* has a total of 48 species, 40% of which are listed in some threat category at the IUCN Red List, but a review of their status in national Red Lists showed an increase in threat category of up to 60%. However, both Red Lists (National vs IUCN) are based on different methodologies with some differences in the applied categorization criteria (see Box 14.1).

Independent of the implemented method, most of the imperiled species among Patagonian lizards were listed within a threat category based on three common factors: (1) small populations, expressed in a small number of individuals and/or a small distributional range; (2) declining populations, expressed in a decline of the number of individuals and/or a decline in the distributional range, and (3) populations severely fragmented and/or species occurring in a small number of localities (criteria A, B, C, and/or D of the IUCN and variable National Distribution of the SUMIN index, see Box 14.1).

Most of Patagonian lizard species are endemic and/or specialists, with restricted ranges, and it is well known that these kinds of species are commonly the most affected by human-related threats (Işik 2011). This is in coincidence with the paradigms of the small populations and the declining populations from the Conservation Biology discipline. In this regard, any management aimed at ensuring the long-lasting viability of these species should mainly be focused on stopping population declines by alleviating main threats and then to recover populations until reaching a stable population size. For this reason, it is very important to firstly know which threats are affecting Patagonian lizards as a way to start planning how to mitigate them.

Box 14.1: Methods Used to Categorize Patagonian Lizards at National and International Red Lists

The National Red List of Patagonian lizards was based on the methodology proposed by Reca et al. (1994) with some modifications (see Lavilla et al. 2000; Giraudo et al. 2012), at least for the Argentinean species, which represents approximately 85% of all lizards' species inhabiting this region. This method depends upon the estimation of the SUMIN index for each species, which is based on assigning standardized values in a qualitative way to six variables (Avila et al. 2013). These variables are (1) national distribution and degree of endemism, (2) ecological rarity, (3) human effects, (4) reproductive potential, (5) size, and (6) abundance. Each variable can have a value from 0 to 5 (5 being the worst value in terms of conservation), and the sum of these variables for each species represents the SUMIN index. The distribution of SUMIN values for all the assessed species is then used to establish a limit value after which a species is considered as threatened. For this reason, this method is sensitive to the number of species assessed. On the other hand, the method applied by the IUCN can determine a threat category on the basis of few variables, as long as a predefined threshold was reached. In this last case, each assessment is species-specific, thus this method is not affected by the number of species assessed. Since both methods have strengths and weaknesses, they can be applied in a complementary way, in order to achieve a deeper understanding about the conservation status of a group of species.

14.3 What Is Threatening Patagonian Lizards?

Nonnative people were the first to inhabit the vast land of Patagonia (most of them immigrants from the United Kingdom) approximately a century ago. The historical use of the Patagonia region by immigrants was as livestock ranches with a number of domestic animals that overpassed the carrying capacity of the ecosystem. This bad management led to a desertification process that even today is considered one of the most harmful process affecting the steppe habitat, 60% of the Patagonia region (Mazzoni and Vázquez 2009). Later, the increasing and not planned urbanization, the unregulated tourism, and the industrial development originated several new sources of threats for native lizards. However not all these threats are affecting Patagonian lizard species in the same way. Detailed knowledge of which threats are specifically affecting each species is key to start developing action plans aimed at protecting these species and its habitats.

Within the species files recorded at both the national and the international Red Lists, detailed information related to specific threats exists for most of the 56 lizards listed in some threat category. However, 22 species still are listed within a threat category but without a reference to any recognized threat. Within these 22 lizard species, 17 of them are included in the genus *Phymaturus*. These species were listed in a threat category only at national level, mainly because they are herbivorous and viviparous lizards (which is not common among neotropical lizards) with restricted distribution ranges, thus they are assumed to be most sensible to potential disturbances (Chap. 13). As seen in Box 14.1, these features are enough to include species in a threat category following the SUMIN methodology but not by following the one used by the IUCN. For this reason, more research is needed in these species in order to start figuring out what threats are affecting them and in which degree of impact. Regarding the 34 species with recognized threats, we can observe that they are affected by a total of 21 types of threats, grouped in 11 of the 12 categories recognized by the IUCN (unified list for classification of threats affecting biodiversity, IUCN 2018). The most frequent threats recognized as affecting Patagonian lizards are related to energy production and mining with 20% of the species affected; agriculture and aquaculture, reaching 20% of the species affected; and residential and commercial development with 13% of the species affected (Table 14.2).

It is important to highlight two threats that may potentially affect Patagonian lizards, related to two governmental projects still not implemented. The first one is the construction of a nuclear plant, projected for northeastern Patagonia (near to the Atlantic coast), and the second one is a hydroelectric dam projected for central western Patagonia, near the Andean mountain range. In the case of dams, a negative effect was already recorded for some threatened Patagonian lizards (Mella and Nunez 2017). For this reason, in case these projects are effectively implemented, the development of a monitoring program for target species is highly recommended, as a way to promote rapid conservation responses when necessary.

14.4 Priority Species for Conservation

It is clear that the biodiversity of the Patagonian lizards is under risk, and if we do not focus on conservation efforts, many populations could decline and even go extinct in a short period of time. However, given that conservation funds are limited, managers must decide where and how to invest (Pimm et al. 2001). In this frame, biologists and managers have developed methods to prioritize conservation efforts (Margules and Usher 1981; Usher 1986; Mindreau et al. 2013) mostly based on priority species and/or areas. In this section we will focus on six priority Patagonian lizard species that must be urgently considered as target in conservation programs. These species are listed as critically endangered at the national and/or the international Red Lists. This category means that a species will probably go extinct if the causes associated to its decline do not cease or diminish under a significant threshold, thus we also will deepen on which are these specific threats and how we can stop them.

Table 14.2 Number of species of each genus affected by different types of threats (the same species can be affected by more than one threat)

	Number of species	Urban development	Agriculture and aquaculture	Energy production and mining	Transportation and service corridors	Biological resource use	Human intrusions and disturbance	Natural system modifications	Invasive and problematic species	Pollution	Geological events	Climate change and severe weather
Pristidactylus	4	1	3	2	1	3	1	1	1	1	0	0
Phymaturus	27	1	3	5	2	0	0	1	0	3	3	1
Liolaemus	22	7	5	7	3	1	4	1	2	2	4	0
Diplolaemus	3	0	0	0	0	1	0	0	0	0	0	0

The item urban development includes residential and commercial development

Liolaemus confusus This species was recently described by Núñez and Pincheira-Donoso (2006). It is known from three closely located sites in Chile. The species is locally common, but it populations are apparently declining due to habitat loss related to the expansion of pine plantations, an exotic habitat that the species reject. It is also threatened by goats overgrazing and firewood extraction (Nuñez 2017). The species was formerly listed as critically endangered at the National Red List (Ministerio del Medio Ambiente 2014), previous to the discovery of a new subpopulation. Later the species was listed as data-deficient at the IUCN Red List (Nuñez 2017), making its real status unclear until more information is gathered. Remarkably, a "preventive rescue" of 20 specimens was carried out when the 2017 Chilean forest fires approached to the type locality, the only time that such protection protocol has been carried out in Liolaemidae (Ramírez-Álvarez et al. 2017).

Conservation Actions Needed or in Course Since the species does not occur in any protected area, it is recommended to conduct actions oriented to protect its habitat and to mitigate main threats.

Liolaemus curis This species is endemic to rocky areas of Andean shrublands in Chile (Termas de Flaco and Damas River) with a very small extent of occurrence of 10 km^2 (see IUCN Nature Serve 2017 for a detailed description of this term). The species was listed as critically endangered at the IUCN Red List (Mella and Nunez 2017) and the Chilean Environmental Ministry (Ministerio del Medio Ambiente 2014), mainly because most of its habitat was completely destroyed by hydroelectric dams, reducing the current population to just a few individuals (Mella and Nunez 2017).

Conservation Actions Needed or in Course Although a group of individuals were successfully translocated to a suitable habitat previous to the development of a hydroelectric plant, this habitat was also lost because of another hydroelectric project (Ministerio del Medio Ambiente 2014). A reintroduction program based on ex situ management would help this species recovery as long as new habitats are found.

Liolaemus cuyumhue This species is only known from its type locality, a small sand dune ecosystem located in Bajo de Añelo (Patagonia Argentina). Its habitat is currently being degraded by intensive oil and gas exploration and exploitation. A recent oil and gas project within the range of this species, which is based on fracking, is planned to be conducted at this species' habitat. Not only this big project but also its consequent activities (new rigs, tracks, and roads) could bring this species to the edge of extinction. For this reason, *L. cuyumhue* is listed as critically endangered at the IUCN Red List (Avila 2016) and as vulnerable at the national Red List (Abdala et al. 2012). *Liolaemus calliston*, a syntopic species recently described (Avila et al. 2017) from the same locality, could be in the same category.

Conservation Actions Needed or in Course A recent news article published in one of the most important newspapers in Argentina discussed a potential revision of the Vaca Muerta project due to the potential extinction of this species (Kacoliris, personal observation). However, considering the expected income of this oil and gas extraction, it does not look like this report is going to change the course of the project. In this context, the search for new habitats for translocating individuals is highly recommended.

Liolaemus hermannunezi This species is known only from the type locality, near Los Barros, Biobío Region, Chile (Pincheira-Donoso and Scolaro 2007; Abdala et al. 2012), its presence in Argentina being uncertain. An international highway planned between Chile and Argentina will cross through its range causing habitat fragmentation and potential roadkills. The species is also thought to be strongly affected by volcanic activity and fires in the region. For these reasons, this lizard was listed as critically endangered at the National Red List (Ministerio del Medio Ambiente 2014). However, given the lack of enough evidence, the species was later listed as data-deficient at the IUCN Red List (Garin et al. 2016).

Conservation Actions Needed or in Course There are no ongoing specific management actions in place aimed to protecting this lizard. The construction of pathways for wildlife could help in reducing the adverse effects of the planned highway.

Liolaemus rabinoi The current area of occupancy of this species is smaller than 4 km^2 (see Nature Serve IUCN 2016 for a detailed description of this term). A hydroelectric dam destroyed the previously known habitat of this species, and it was assumed extinct. A new population was found in sand dunes that are heavily disturbed by the unregulated circulation of off-road vehicles, including rally competitions (Abdala et al. 2017). For these reasons and the fact that this lizard does not occur in any protected area, the species was listed as critically endangered in the IUCN and in the national Red Lists (Abdala 2016; Abdala et al. 2012).

Conservation Actions Needed or in Course Some attempts were conducted to avoid circulation of vehicles in the area, including a change in the route of the Dakar Rally. However, local people still drive on the habitat. Effective prohibition of vehicles on these sandy habitats and the creation of a protected area are highly needed. Translocation of individuals to safer habitats could also improve current status of this species by promoting the establishment of new populations.

Phymaturus vociferator This species is endemic to Chile, with an extent of occurrence of nearly 74 km^2. Its whole population is restricted to one location. Although the population is located within a National Park, a binational project aimed at connecting Argentina and Chile through a highway would threaten the species (Avilés et al. 2017). The road could lead to a decline in the extent and quality of the habitat of this lizard and, even worst, to the species' extinction. For this reason *P. vociferator* was listed as critically endangered at the National Red List and as vulnerable at the IUCN Red List (Avilés et al. 2017).

Conservation Actions Needed or in Course This species is found in Parque Nacional Laguna del Laja. Still, no ongoing conservation actions are taking place to prevent the effects of the planned highway. The construction of pathways for wildlife could help reduce the adverse effects of the highway.

In summary, a total of six lizard species are listed as critically endangered at least in one of the Red Lists. However, the status of two of these species, *L. confusus* and *L. hermannunezi*, was recently changed to data-deficient, making its real status unclear until new information is gathered. Among the other four species, two of them are endemic to Argentina (*L. cuyumhue* and *L. rabinoi*), and two of them are endemic to Chile (*L. curis* and *P. vociferator*). Urgent actions are required to avoid the extinction of these four species but without losing sight of the remaining species. In a regional context of increasing threats (e.g., highways, hydroelectric plants, oil and gas extraction, etc.), it is expected that several of the species currently listed as endangered or vulnerable will be moved to a critically endangered category. At the same time, data-deficient and species not yet assessed might fall in any threat category in the short term. Thus, not only specific actions for priority species but also bigger and more ambitious actions are needed to preserve a higher number of Patagonian lizard species in the wild.

14.5 Priority Areas for Conserving Patagonian Lizards

Which areas are better to protect lizards in Patagonia? As seen before, the answer to this question will depend on the conservation target—a species or a group of species, but in any case, priorities among different areas should be established on the basis on predefined criteria. However, even when targets are known and priorities are established, to design a protected area is very difficult, and the real implementation of that area is even harder. A lot of variables must be attended, and many times, the designated areas tend not to be the ones identified as priorities in scientific studies. Even so, researchers continue doing their best trying to develop methodologies that include the most detailed information for a better prioritization process (see Box 14.2). In this section, we provide some basic but important information to help in identifying some priority areas for conservation of Patagonian lizards.

Box 14.2: Some Methods Used to Establish Conservation Priorities
Prioritization is commonly related to the fact that conservation resources are limited. Thus, it is necessary to decide where to focus conservation efforts. There are several ways to determine priorities among areas when the aim is to protect species. A simple approach to prioritizing is to assess species richness

(continued)

Box 14.2 (continued)

among potential areas. The higher the number of species present in a specific area, the higher the priority for conservation. In other cases, the objective of a protected area can be to conserve a single highly threatened species. To integrate both approaches, some methods that consider the differential contribution of endangered species to the overall richness were developed (Fattorini 2006). Several other factors are commonly considered in prioritization (e.g., politics, opportunities, social context, land availability, and degree of disturbance, among others), promoting the development of methods aimed at easing the decision-making process to managers (Álvarez-Berastegui et al. 2014; Kacoliris et al. 2012). Moreover, newer approaches have to consider future changes in habitats due to climate change. It is clear that the problem of determining priority areas for conservation has been a prevailing one among specialists and managers, and there is not just one solution. Instead, new methods must be adaptive and flexible enough to not only be useful but also feasible for solving specific problems.

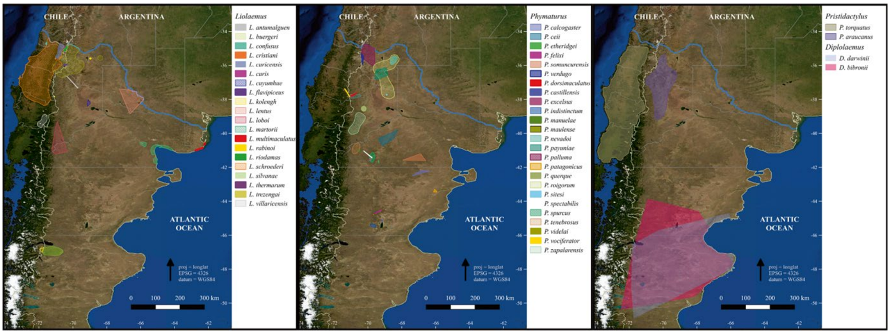

Fig. 14.1 Known ranges for priority lizard species inhabiting Patagonia

A simple but logical approach is to assume that the distributional range of priority species (i.e., the species with the higher extinction risk) should be a priority area. In Fig. 14.1 we represented the known distributional ranges for Patagonian lizards listed as threatened at national and/or IUCN Red Lists (i.e., vulnerable, endangered, or critically endangered). At first glance, this clearly shows that the aim of protecting all these threatened species by setting protected areas that encompass their ranges is very ambitious. However, if we focus just on the most threatened species (i.e., the four listed as critically endangered—*L. cuyumhue*, *L. rabinoi*, *L. curis*, and *P. vociferator*), the total area to protect, based on their extent of occurrence and area of occupancy, would be less than 100 km^2. Unfortunately, as seen in the previous section for some of these species, the economic interests on the lands where they inhabit make very unlikely the creation of protected areas there.

Another approach is provided by Corbalán et al. (2011), who defined priority areas based on the core area of the geographical distribution of the Patagonian lizards (with a high probability of presence). In the method proposed by these authors, key conservation areas for Patagonian lizards are defined based on a systematic planning with decision support tools (e.g., Marxan and Zonation). These algorithms consider both biological and socioeconomic data along spatial discretized planning units (Watts et al. 2009; Lehtomäki and Moilanen 2013). This type of design and planning of protected areas allow decisions through reproducible and perfectible analysis on both temporal and spatial scales (Watts et al. 2009; Delavenne et al. 2012). The authors conclude that the current reserve network fails in protecting at least 10 out of 60 lizard species included in the study and that in order to protect at least 5% of the distributional ranges of these lizards, the reserve network should increase its area by 3.7%.

An alternative approach to determine priority areas in Patagonia includes several sources of information such as geomorphology, fauna, vegetation, ecology, paleontology, and archaeology of the region (Chehébar et al. 2002). Within the fauna category, the authors considered 82 Patagonian lizard species, among several other vertebrates. Some results of this detailed study were congruent with those obtained by Corbalán et al. (2011), indicating that lizards can act as surrogate species for other taxa (i.e., priority areas for lizards can be similar to priority areas for vertebrates). Even more, some of the priority areas for lizards recognized in Corbalán et al. (2011) are congruent with priority areas selected based on the geomorphology and landscape in Chehébar et al. (2002), thus indicating that in some situations, protecting lizards can lead to the conservation of other values than fauna alone.

Regrettably, as observed before, the gap between the identification of a priority area and effectively protecting that area is usually extremely large, most of the time nearly impossible. Luckily, several types of legally protected areas exist in Patagonia. These areas have different categories including National Parks, National Reserves, Provincial Reserves, Biodiversity Refuges, Private Reserves, and others. National Parks are the most stable because they depend on their own autonomous government and have designated management and control resources. These National Parks play an important role in protecting suitable areas for a high number of Patagonian lizard species (Chebez et al. 2005). In a controversial way, *P. vociferator* is the only critically endangered species that is currently protected within a National Park (Laguna de Laja). Future efforts should promote the creation of new protected areas to ensure a better conservation of some of the most threatened lizards in Patagonia.

14.6 The Challenge of Conserving Lizards: What We Can Do?

The conservation of lizards represents a big challenge and in many cases is even greater than in other groups of vertebrates, because these small animals are not seen as charismatic species (Chap. 2). This situation not only hinders the access to conservation resources but also makes it difficult for people to engage in lizard conservation. Fortunately, the engagement of people is possible (e.g., sand lizard *L. multimaculatus*, Kacoliris et al. 2012) but requires conservationists to be creative. Even so, people's engagement alone is not enough to stop lizards' decline. The conservation problems affecting Patagonian lizards are too complex, so effective protection of these species can only be addressed by a combination of pragmatic actions.

We already have a combination of tools and guides to use in order to improve the conservation of endangered lizards and their habitats, but none of them can be considered a "silver bullet." Actions that work with one species or area might not with other species and even with the same species but in a different scenario. For this reason, these guidelines should be adapted to particular situations, considering the future (and sometimes unexpected) changes and always considering some degree of uncertainty. Adaptive management has proven to be a good strategy since it allows producing scientific knowledge at the same time that the conservation actions are applied and tested. But also, the monitoring should be a key component of any conservation project in order to help address unexpected alterations in a changing world (i.e., the unexpected should be expected).

We have to find creative ways to increase the awareness about lizards' problems with the aim of promoting a behavioral change in people, creating and reinforcing empathetic feelings. In this sense, it is important to work in creating alternatives for local communities in order to replace unsustainable activities with sustainable ones, without affecting or even by improving their annual incomes. A good example of this goal is ecotourism, an activity that is already taking place in several places of Patagonia. However, regulations must be applied in order to benefit local communities over big enterprises, as a way to promote long-lasting sustainability. Furthermore, we have to get more people to be involved in activism as a means to create and to change governmental decisions. Several current environmental policies are taken without any scientific basis and with a clear negative effect on biodiversity. To cite some examples, at some provinces of Patagonia, native species like the cougar and the guanacos were declared as plague, while at the same time some invasive and highly harmful species like trout are being bred and introduced in native habitats by law. When more people start to demand governments to take care of the environment, some of these nonsense can be reversed.

The future of Patagonian lizards is uncertain. Known and unknown threats, in addition to climate change, will probably cause several species to go extinct in the short- and midterm. However, we are still on time to make a substantial change, by combining research and management and by promoting appropriate government decisions. If we do, we can probably increase the viability of several endangered Patagonian lizards and their habitats. We are on a breakpoint on Earth's history that requires plenty of commitment by our part. For those of us who love lizards, is time to get down to work.

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