Chapter 9
Diversification and Evolutionary Histories of Patagonian Steppe Lizards

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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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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
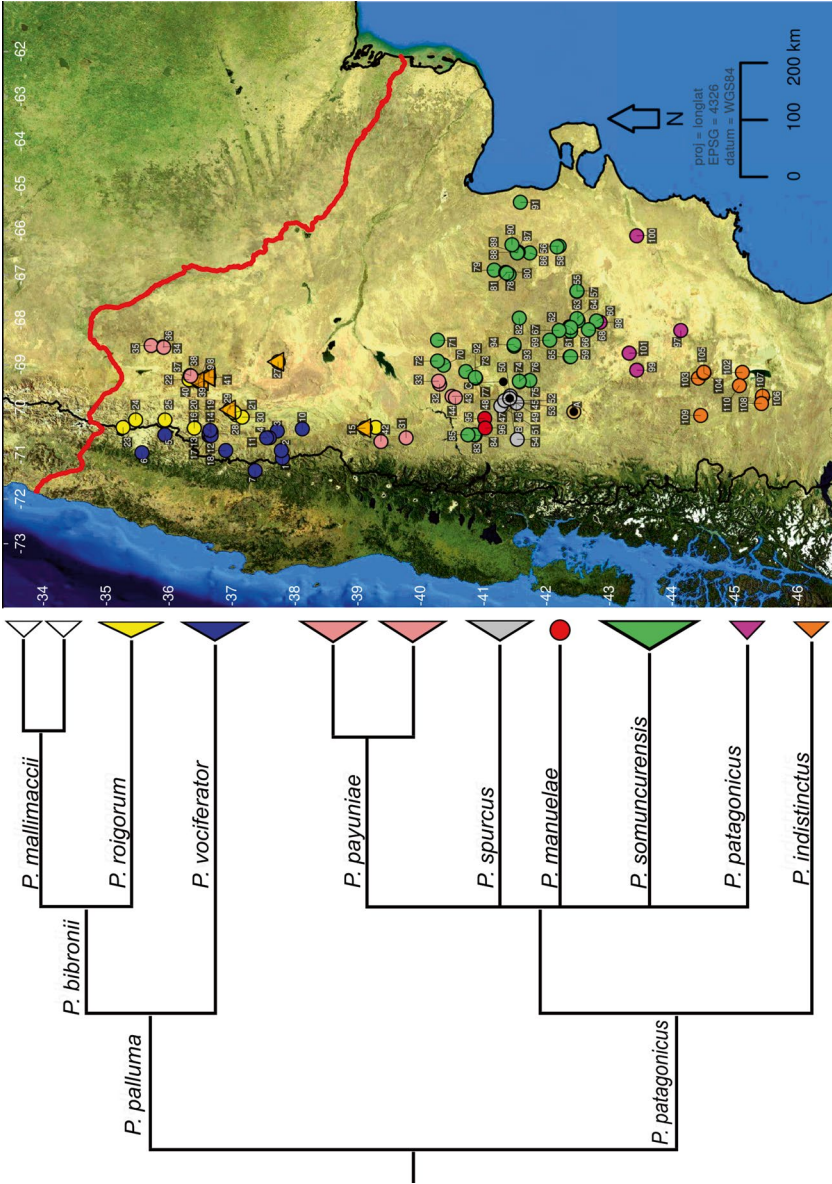
Fig. 9.1 Geographic distribution of *Phymaturus* species in Patagonia based on georeferenced localities with voucher numbers, arranged based on updated systematic studies summarized in tree on the left. Clades are color-coded with localities. The five localities where one species of the *palluma* and 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. 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)
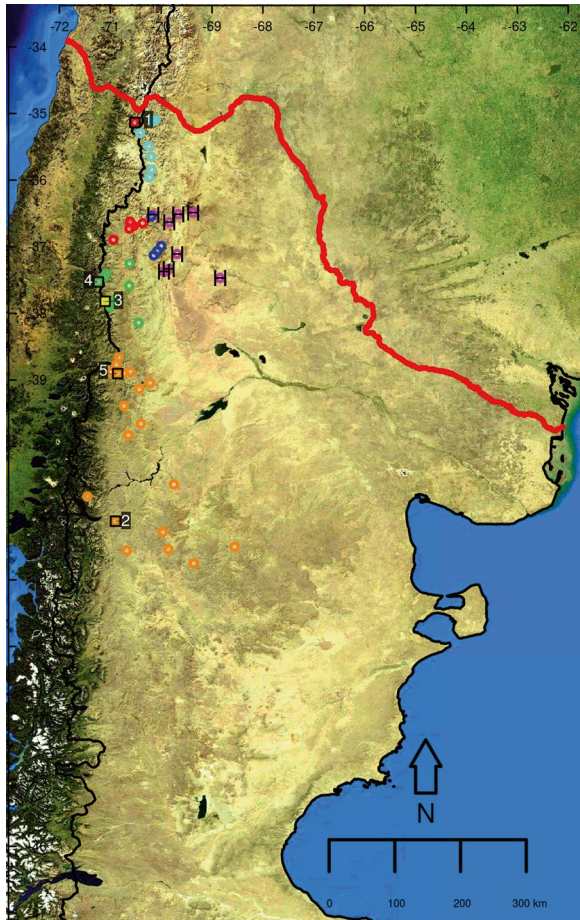
A more densely sampled phylogeographic study of the *L. elongatus* complex (Medina et al. 2017), coupled with new species descriptions (Abdala et al. 2010; Avila et al. 2010, 2012, 2015), increased the number of recognized species in Argentinean Patagonia to nine, plus three candidate species (Fig. 9.3). 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
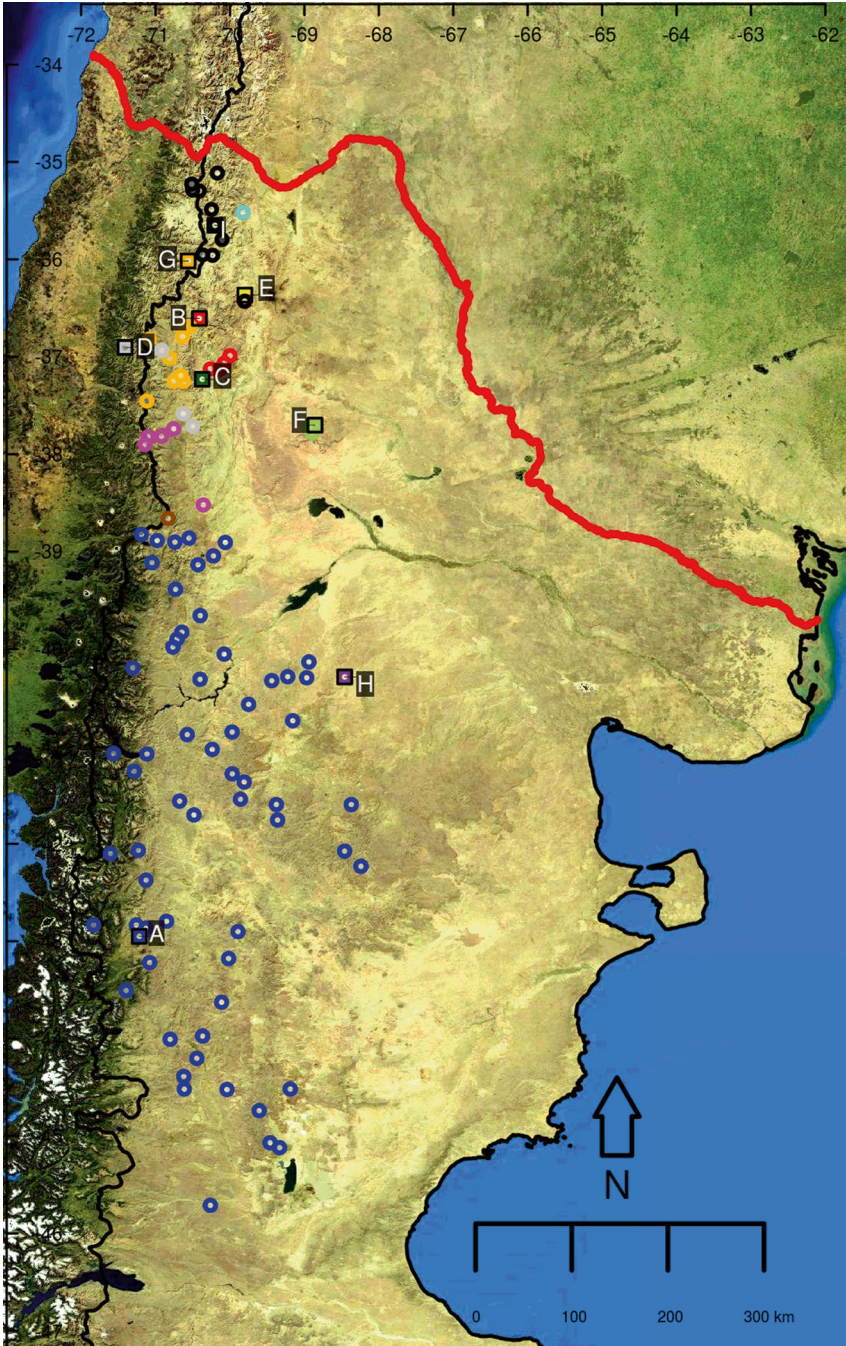
Fig. 9.3 Distribution area for the *Liolaemus elongatus* species group based on vouchered individuals used in phylogenetic and phylogeographic analyses. Letters represent type localities and colored circles mark georeferenced localities for each recognized taxon; A: *L. elongatus*, blue; B: *L. antumalguen*, 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
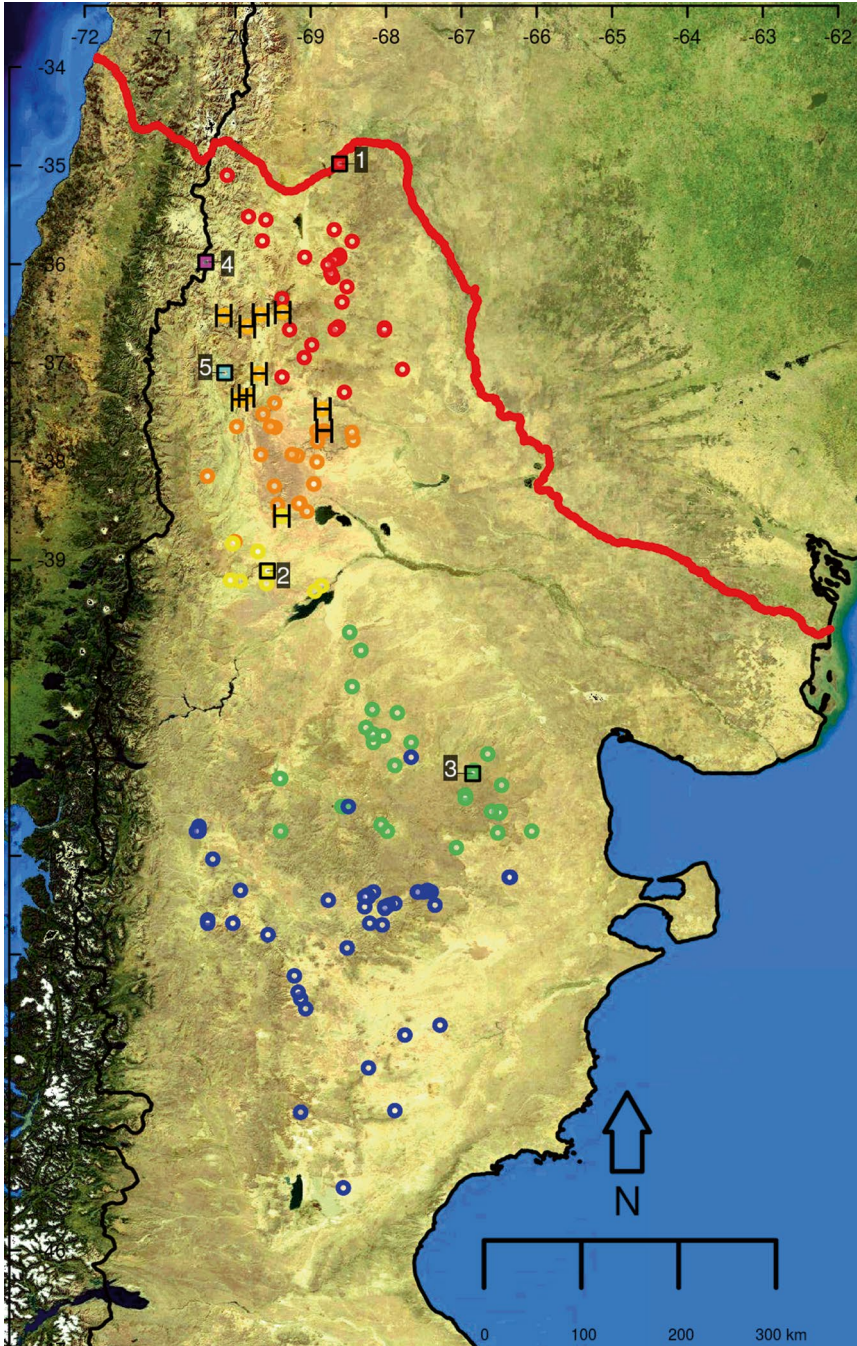
Fig. 9.4 Distribution area for the *Liolaemus petrophilus* species group based on vouchered individuals used in phylogenetic and phylogeographic analyses, and for the *L. punmahuida* clade. Numbers represent type localities and colored circles mark georeferenced localities for each

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
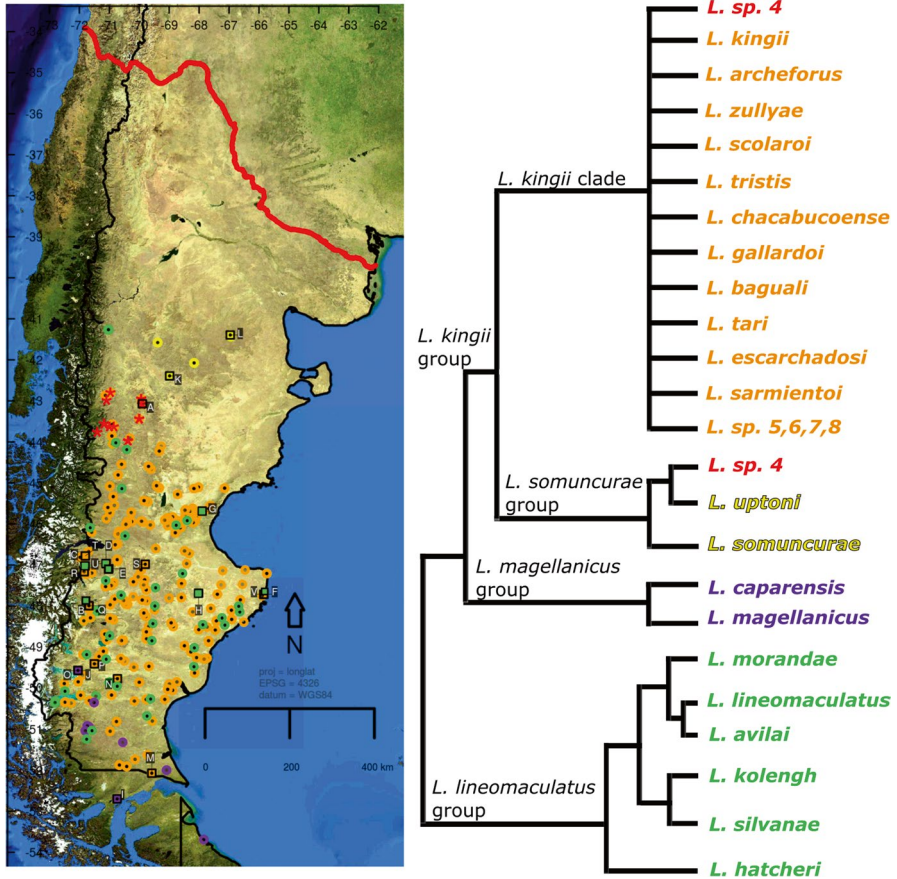
Fig. 9.5 Distribution area for the *Liolaemus lineomaculatus* section based on vouchered individuals used in phylogenetic and phylogeographic analyses. Letters represent type localities and colored circles mark georeferenced localities. The *L. lineomaculatus* species group is colored in green: B, *L. 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)
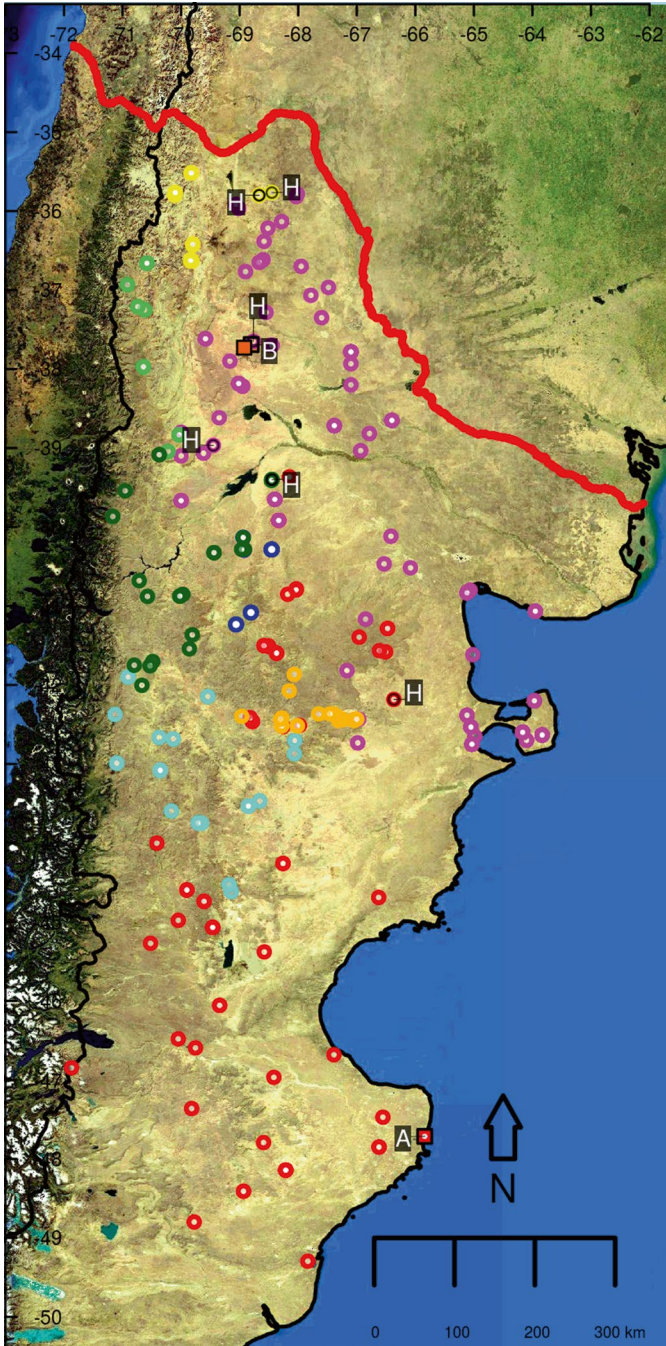
Fig. 9.6 Distribution area for the *L. bibronii* species complex and *L. gracilis*, based on phylogenetic and phylogeographic analyses. A: type locality of *Liolaemus bibronii* (sensu stricto, red

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
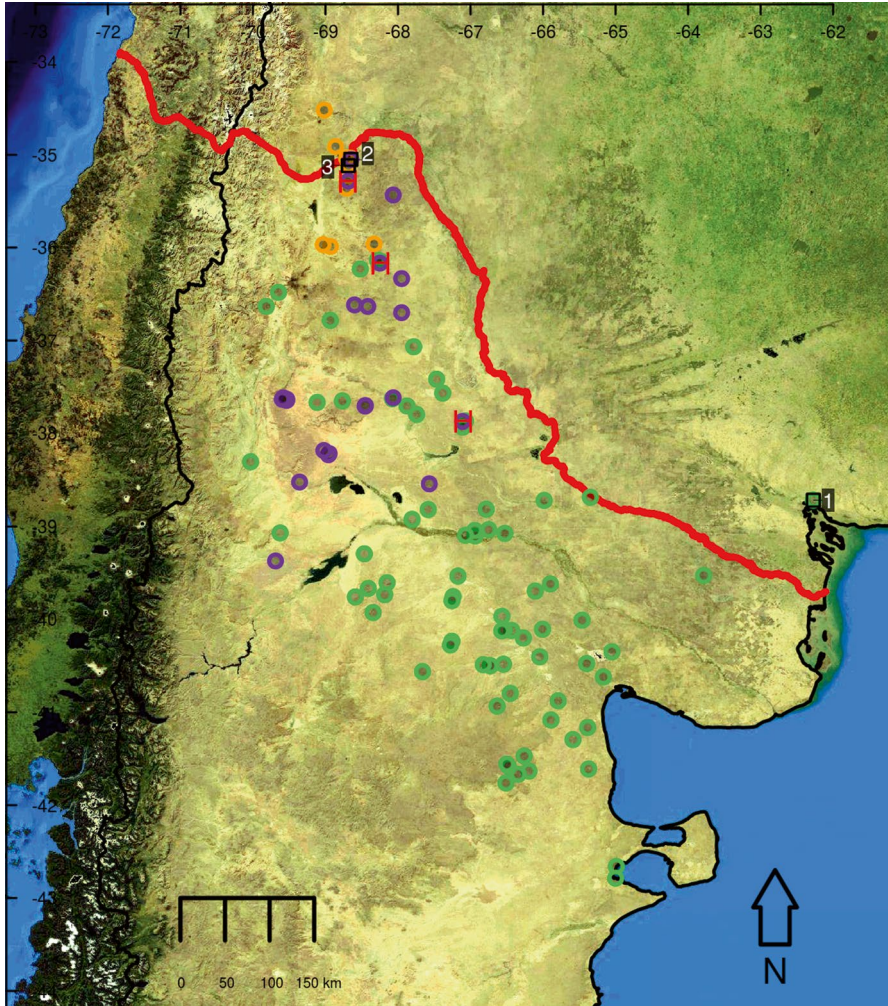
Fig. 9.7 Distribution area for *Liolaemus darwinii*, *L. grosseorum* and *L. parthenos*, based on phylogenetic and phylogeographic analyses. Numbers represent type localities and colored circles mark georeferenced localities for each taxon. 1, *L. darwinii*, green; 2, *L. grosseorum*, purple; 3, *L. 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*,
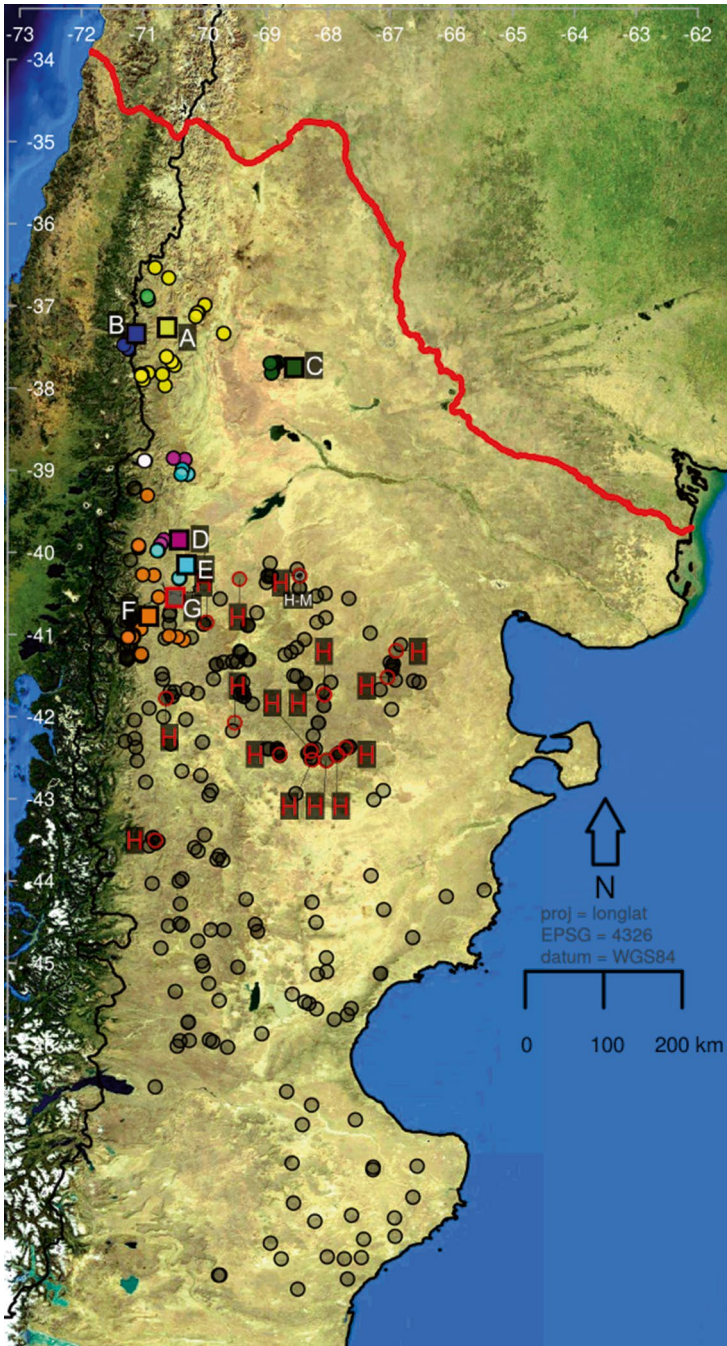
Fig. 9.8 Distribution area for the *Liolaemus rothi* species group based on phylogenetic and phylogeographic analyses. Letters represent type localities and colored circles georeferenced localities

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

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)
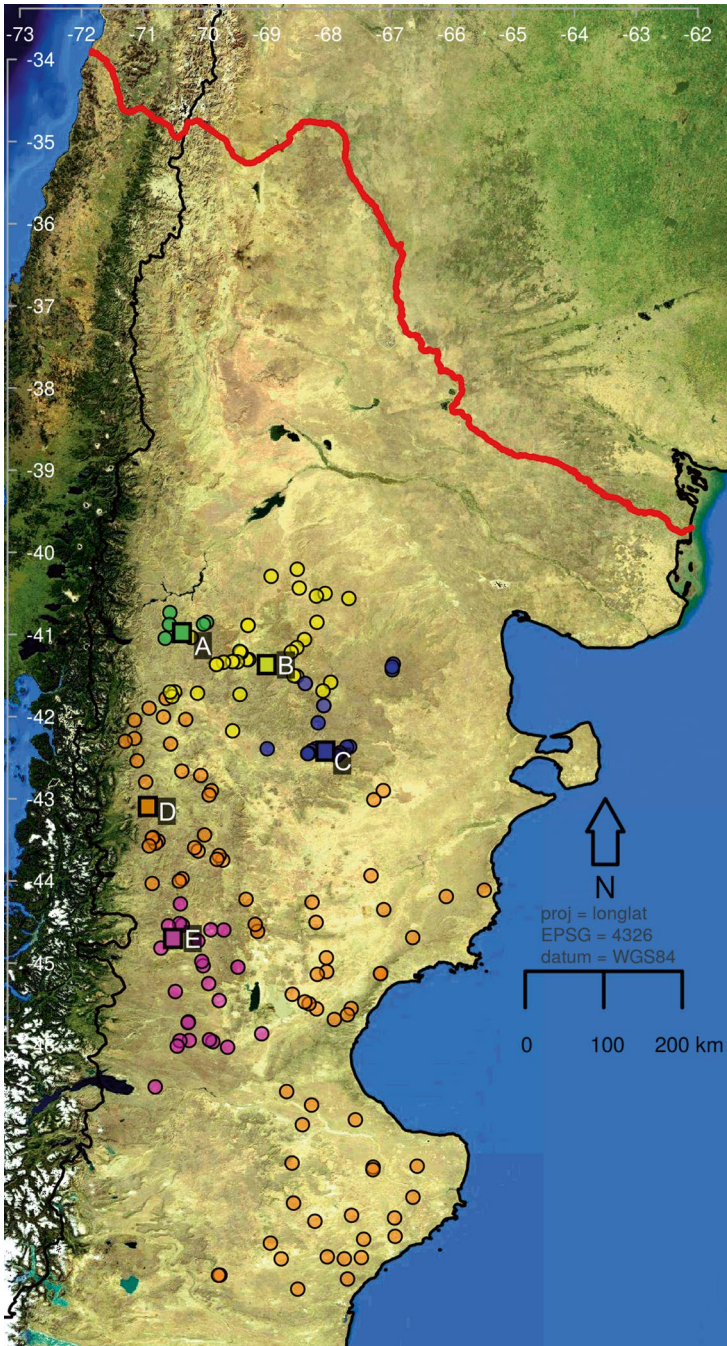
Fig. 9.9 Distribution area for the *Liolaemus boulengeri* species group based on phylogenetic and phylogeographic analyses. Letters represent type localities and colored circles mark georeferenced localities for each taxon. A, *L. tehuelche*, green; B, *L. inacayali*, yellow; C, *L. telsen*, dark purple; 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,
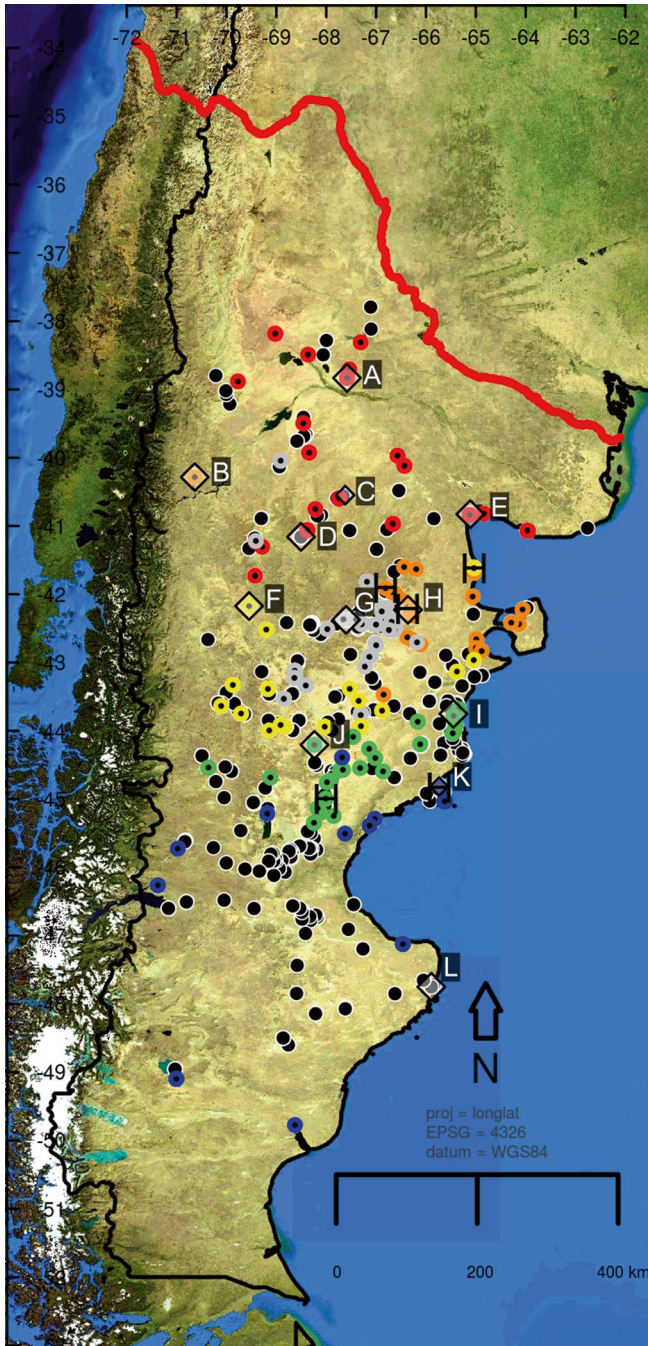
Fig. 9.10 Distribution area for the *Liolaemus fitzingerii* species group based on phylogenetic and phylogeographic analyses, represented with dark blue circles. Based on genomic ~900 SNPs, Grummer (2017) inferred 6 groups, color-coded and corresponding to different combinations of the 12 available species 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:
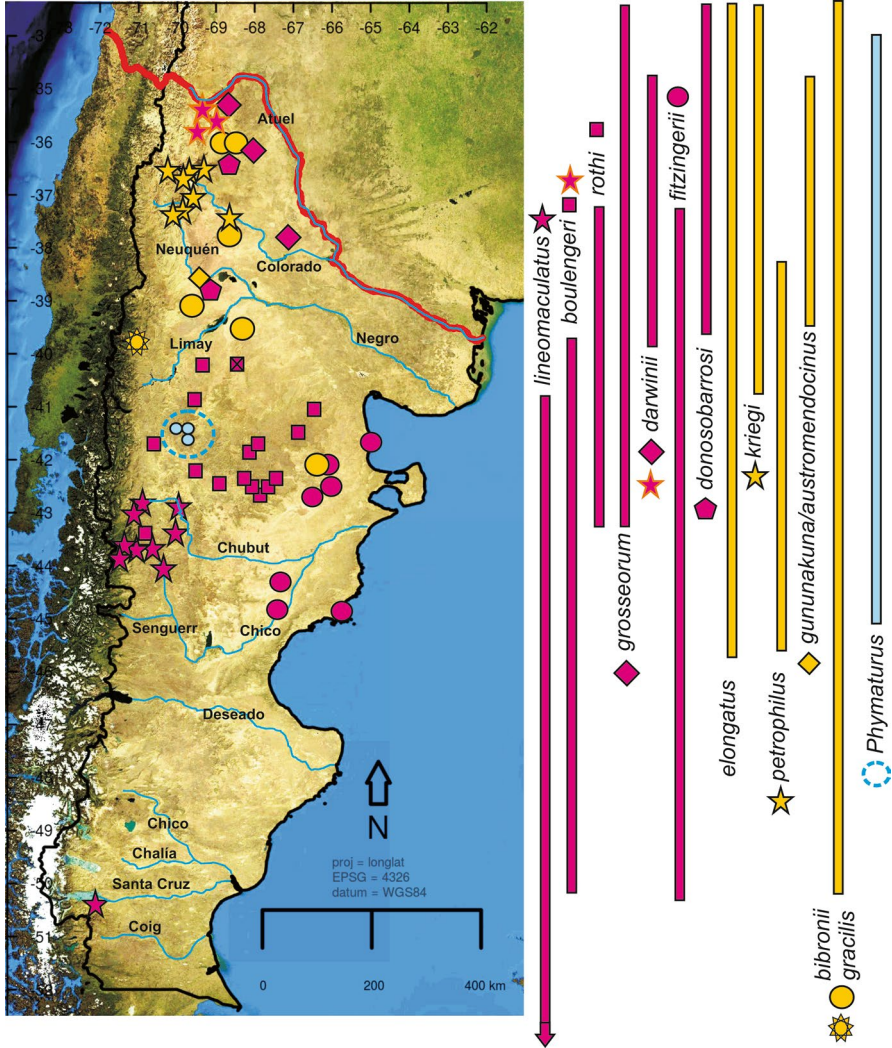
Fig. 9.11 Hybridization hypotheses in *Liolaemus*. Main *Eulaemus* clade: purple, *Liolaemus* sensu stricto: yellow. Stars: populations/species of possible hybrid origin. Yellow star with 12 points: *L. abdalai*. Purple stars with orange border: *L. parthenos*. Pink square with "X": *L. rothi* mosaic 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

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
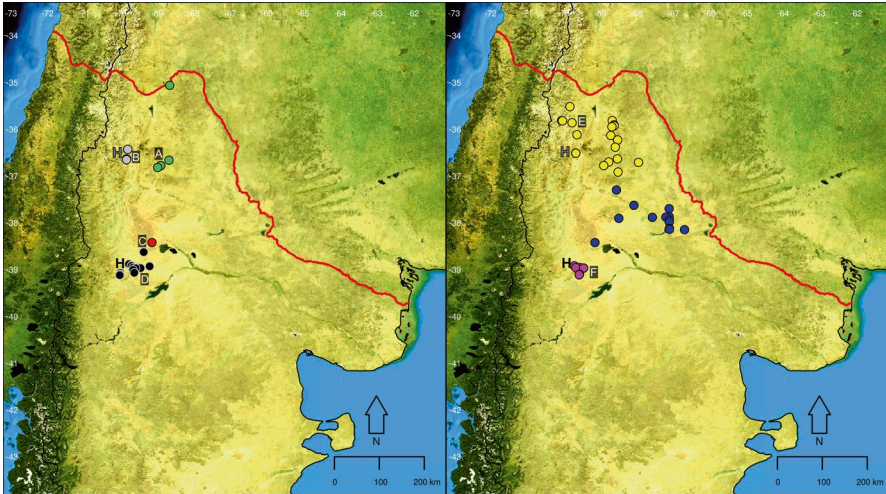
Fig. 9.12 Distribution area for the *Liolaemus donosobarrosi* species group based on phylogenetic and phylogeographic analyses. Letters represent type localities and colored circles mark georeferenced localities for each taxon A, *L. donosobarrosi*, green; B, *L. puelche*, grey; C, *L. calliston*, red; 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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