The Patagonian Herpetofauna

José M. Cei

Instituto de Biología Animal
Universidad Nacional de Cuyo
Casilla Correo 327
Mendoza, Argentina

Reprinted from:

DUELLMAN, WILLIAM E. (ed.). 1979. The South American Herpetofauna: Its origin, evolution, and dispersal. Univ. Kansas Mus. Nat. Hist. Monogr. 7: 1–485.

13. The Patagonian Herpetofauna

José M. Cei

Instituto de Biología Animal
Universidad Nacional de Cuyo
Casilla Correo 327
Mendoza, Argentina

The word Patagonia is derived from the term "Patagones," meaning big-legged men, applied to the tall Tehuelche Indians of southernmost South America by Ferdinand Magellan in 1520. Subsequently, this picturesque name came to be applied to a conspicuous continental region and to its biota.

Biologically, Patagonia can be defined as that region east of the Andes and extending southward to the Straits of Magellan and eastward to the Atlantic Ocean. The northern boundary is not so clear cut. Elements of the Pampean biota penetrate southward along the coast between the Río Colorado and the Río Negro (Fig. 13:1). Also, in the west Patagonian landscapes and biota enter the volcanic regions of southern Mendoza, almost reaching the Río Atuel Basin. The Patagonian region has a wide ecotonal zone with the Chacoan region (Gallardo, this volume). The monte vegetation (Morello, 1958) with its several formations containing numerous subtropical elements extends south to the Península de Valdes; the monte enters the Río Chubut drainage and extends westward to the Río Neuquén, Río Agrio, and Río Limay valleys. South of the Río Negro, the monte associations exist in a system of saline lowlands (*bajos*) and reach irregular spurs of the Meseta de Somuncurá, a typical Patagonian environment (Cei, 1969a,b; Ruiz Leal, 1972). Nevertheless, there is a general, sometimes remarkable, agreement between the phytogeographic boundaries of the Monte-Pampean and the Patagonian regions and the distribution patterns of their herpetofaunas. Herein I emphasize the biota of the Cis-Andean steppe to the near exclusion of the Trans-Andean austral forest ecosystems treated by Formas (this volume).

Patagonia is a region of sedimentary rocks and soils, mostly tablelands subjected to prolonged erosion. Scattered through the region are extensive areas of extrusive basaltic rocks. The open landscape is dissected by transverse rivers descending from the snowy Andean cordillera; drainage is poor near the Atlantic coast. Patagonia is subjected to severe seasonal drought with about five cold winter months and a cool dry summer, infrequently interrupted by irregular rains and floods.

HISTORY OF THE PATAGONIAN BIOTA

In contrast to the present, almost uniform steppe associations in Río Negro, Chubut, and Santa Cruz provinces, during Oligocene and Miocene times tropical and subtropical vegetation occurred along with xerophytic woodlands with luxuriant mesophytic gallery forests. A comparison of the rich Miocene flora of Pichi Leufu, Río Negro (Berry, 1938) with analagous associations from Mirhoja, Chubut; Valcheta, Río Negro; and Río Chalia, Santa Cruz, shows a mixture of mesic tropical elements (*Ficus, Fagara, Nectandra, Tabebuia, Myristica, Sterculia*, tree ferns, *Erythroxylon, Oreopanax, Maytenus*), including climbers (*Buettneria, Banisteria, Bignonia, Cissus, Paullinia, Sapindus, Strychnos*), together with nontropical genera (*Araucaria, Azora, Berberis, Ginkgo, Laurelia, Embothrium, Fitzroya, Libocedrus, Podocarpus, Lomatia, Peumus, Myrceugenia, Drimys*). Most of the latter are characteristic components of the present temperate Valdivian forest. Nevertheless, xeric areas in the Middle Tertiary of Patagonia are suggested by certain paleofloras containing *Schinopsis, Schinus*, and *Cupania*. The former is a significant genus of trees in the subtropical Chacoan region.

Nothofagus forests were widespread in Patagonia in the Eocene and Oligocene, but

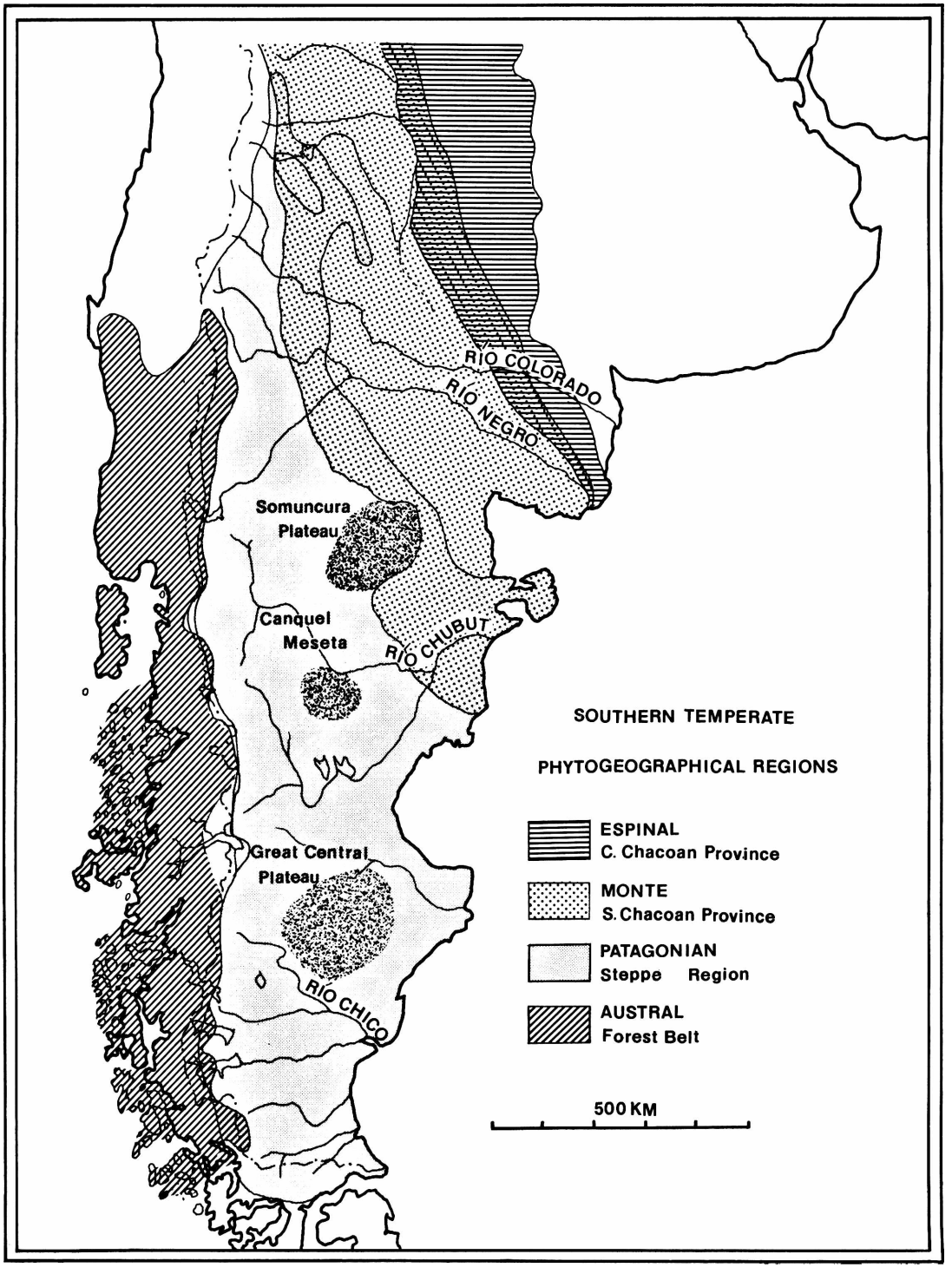

FIG. 13:1. Phytogeographic regions of austral South America.
Regiones fitogeográficas de Sud América austral.

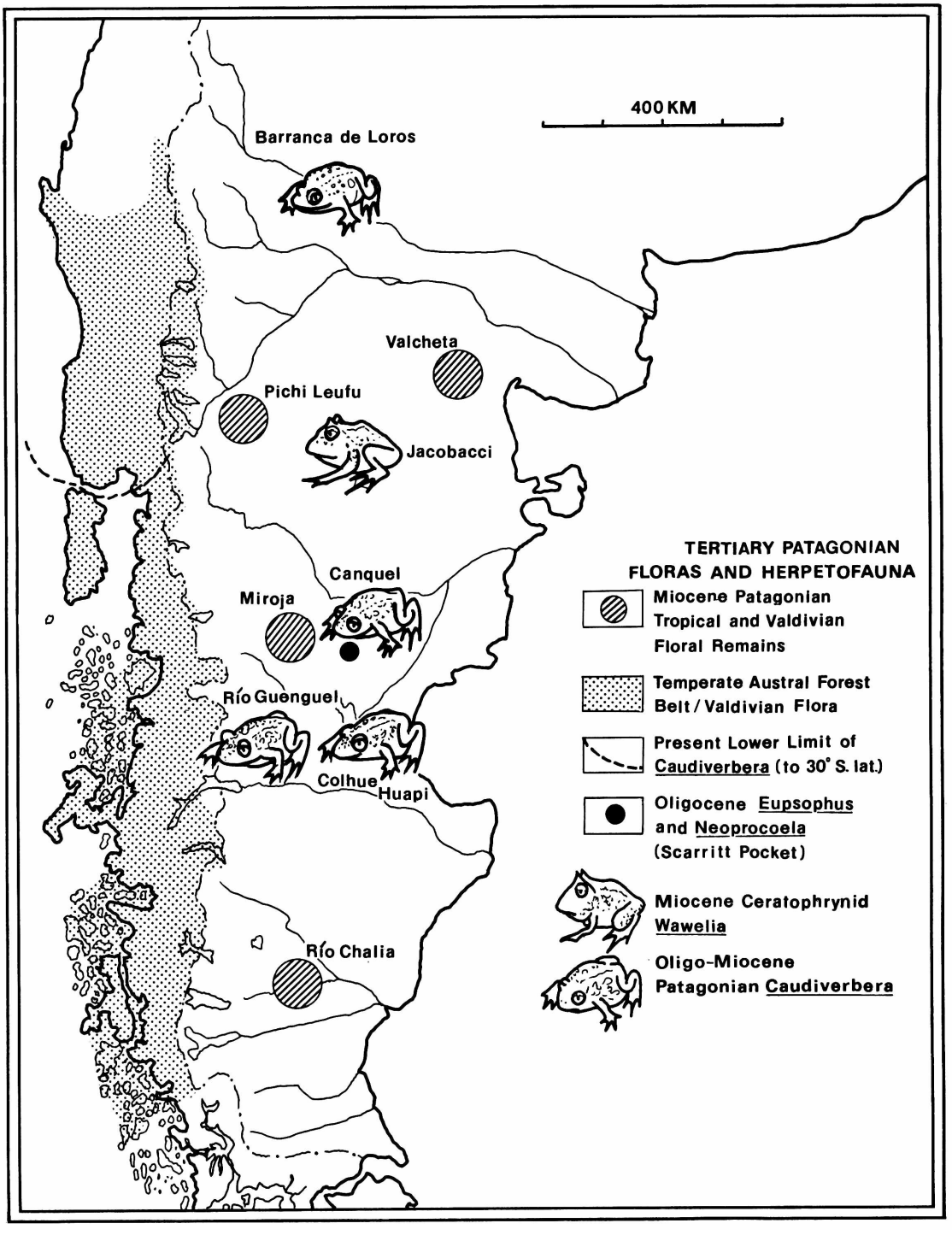

FIG. 13:2. Paleontological records of the lower Tertiary Patagonian flora and of leptodactylid frogs. *Hallazgos paleontológicos de flora patagónica del Terciario inferior y de anuros leptodactylidos.*

these associations decreased and retreated southward and westward in the Middle and Late Tertiary. *Chusquea* bamboo groves occur in Cenozoic deposits at Laguna Hunco, Chubut. Further evidence of paleoclimatic conditions in Patagonia is derived from the extensive paleo-mammal faunas (Báez and Scillato Yané, this volume) and more limited paleo-herpetofaunas (Báez and Gasparini, this volume).

Primitive leptodactylid, ceratophrynine, and bufonid frogs have been recorded by Schaeffer (1949), Chaffee (1952), and Casamiquela (1963) from the Deseadan, early Oligocene Scarritt Pocket Formation (Canquel, Chubut) and from the upper Miocene of Río Negro (Fig. 13:2). The living Chilean frog *Caudiverbera caudiverbera* is almost identical to the fossil frogs of the same genus. A fossil frog from the Oligocene of Chubut referred to *Eupsophus* by Schaeffer (1949) has been considered the same as living *E. roseus*, a species characteristic of the *Nothofagus* forests of southern Chile (Bogart, 1970). These fossils clearly establish the presence of telmatobiine frogs in Patagonia in the Oligocene and Miocene.

The Oligocene *Neoprocoela* was provisionally referred to a *Batrachophrynus* or *Telmatobius*-like leptodactylid stock by Schaeffer (1949). Tihen (1962) considered it to be a species of *Bufo* in the Palearctic *Bufo calamita* group. The fossil was again associated with the telmatobiine genera *Telmatobufo* and *Batrachophrynus* by Lynch (1971). New material from the same formation supports the inclusion of *Neoprocoela* in *Bufo* (Estes, pers. comm.). The placement of *Neoprocoela* in the *Bufo calamita* group has interesting biogeographical implications. Serological evidence (Cei, 1977) supports a relationship between the European *Bufo calamita* and the small *B. variegatus* presently restricted to the austral *Nothofagus* forests of Argentina and Chile (Gallardo, 1962).

The presence of a ceratophrynine frog (*Wawelia gerholdi*) in the Miocene provides herpetological evidence for the southward extent of tropical elements in the Middle Tertiary. Reptilian remains substantiate the long history of tropical elements in Patagonia. The fossil snake *Dinilysia patagonica* from the Upper Cretaceous of Neuquén is related to boids and aniliids that are widespread in tropical South America. Furthermore, boid snakes (*Madtsoia*), crocodilians (*Necrosuchus*, *Sebecus*, *Eocaiman*), and meiolaniid and pelomedusid turtles from Paleocene-Eocene deposits in Chubut are indicative of tropical environments (Gasparini and Báez, 1975). Iguanid (*Erichosaurus debilis*) and teiid (*Diasemosaurus occidentalis*) lizards lived in southern Santa Cruz in the Miocene.

PATAGONIAN FAUNAL REGIONS

Two major faunal regions (habitats) can be defined in Patagonia. These are the northern or ancient region and the southern or Santa Cruz region; the border between these regions is approximately at the Río Chubut at 45°S (Fig. 13:3). These habitats correspond to ancient physiographic areas, the Patagonian Massif and the Deseado Massif, respectively (Figs. 13:4–5). These massifs are ancient structural continental units known as nesocratons (Harrington, 1962). In spite of its less marked subpositive tendency in comparison with the Pampean Massif, the whole region of the Patagonian Massif has been a site of almost uninterrupted accumulation of continental deposits. More rarely it received shallow marine deposits peripherally at times of oceanic transgressions in the Eocene-early Oligocene, middle Oligocene, and middle Miocene. The smaller Deseado Massif had a subpositive tendency even less marked than the Patagonian Massif; accordingly, its relief was often depressed, and during prolonged subsidences it became a sedimentary area like the adjacent pericratonic basins (Harrington, 1962).

The northern or ancient Patagonian region extends through Neuquén, Río Negro, and Chubut provinces (Fig. 13:6). The subcordilleran area in Neuquén is drained by the Río Agrio and Río Neuquén, which flow into the Río Limay, a tributary of the Río Negro. Extra-cordilleran mesetas include the large Meseta de Somuncurá (1000–1700 m eleva-

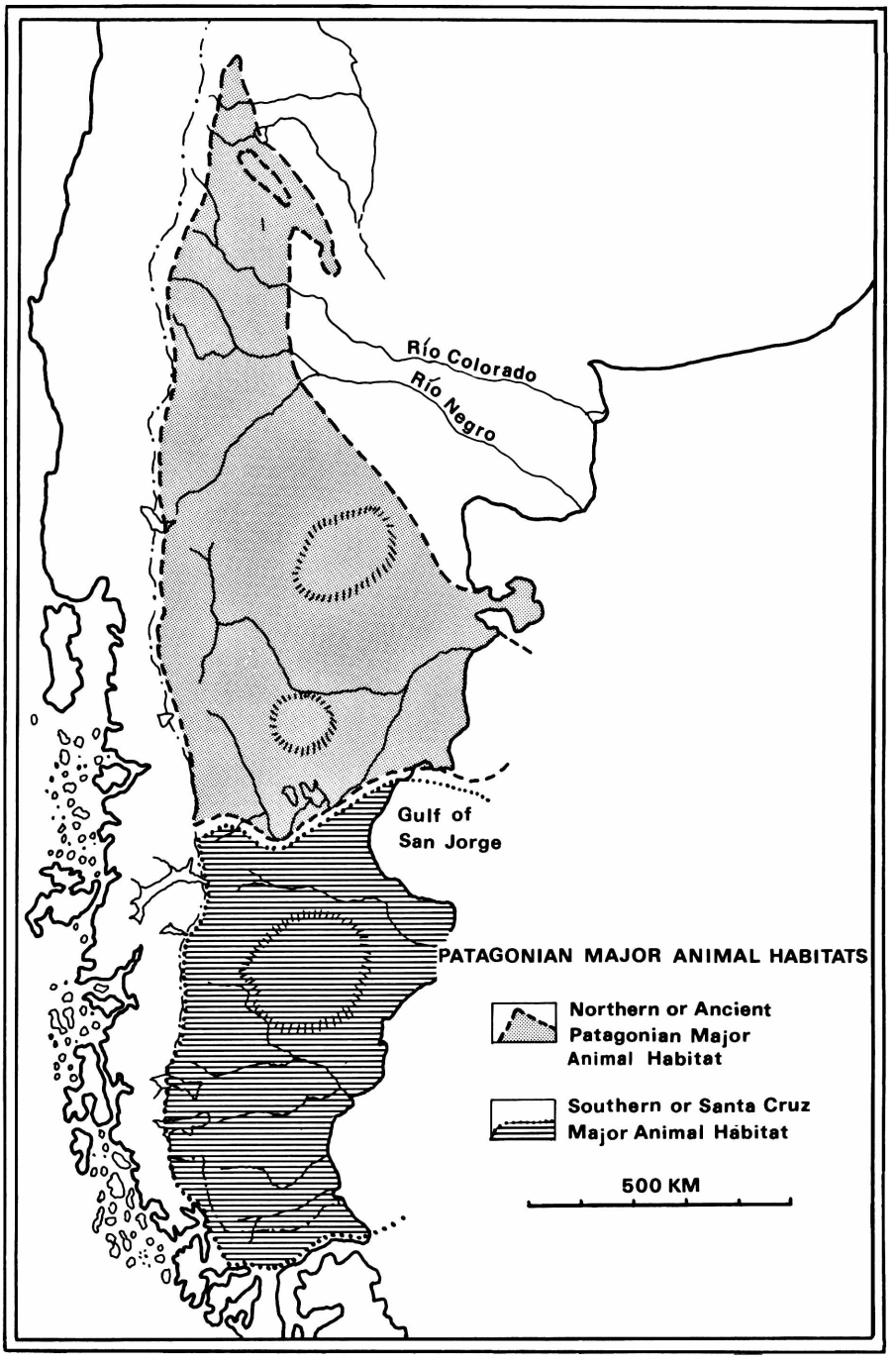

FIG. 13:3. Major herpetofaunal regions of Patagonia.
Regiones herpetofaunísticas fundamentales de Patagonia.

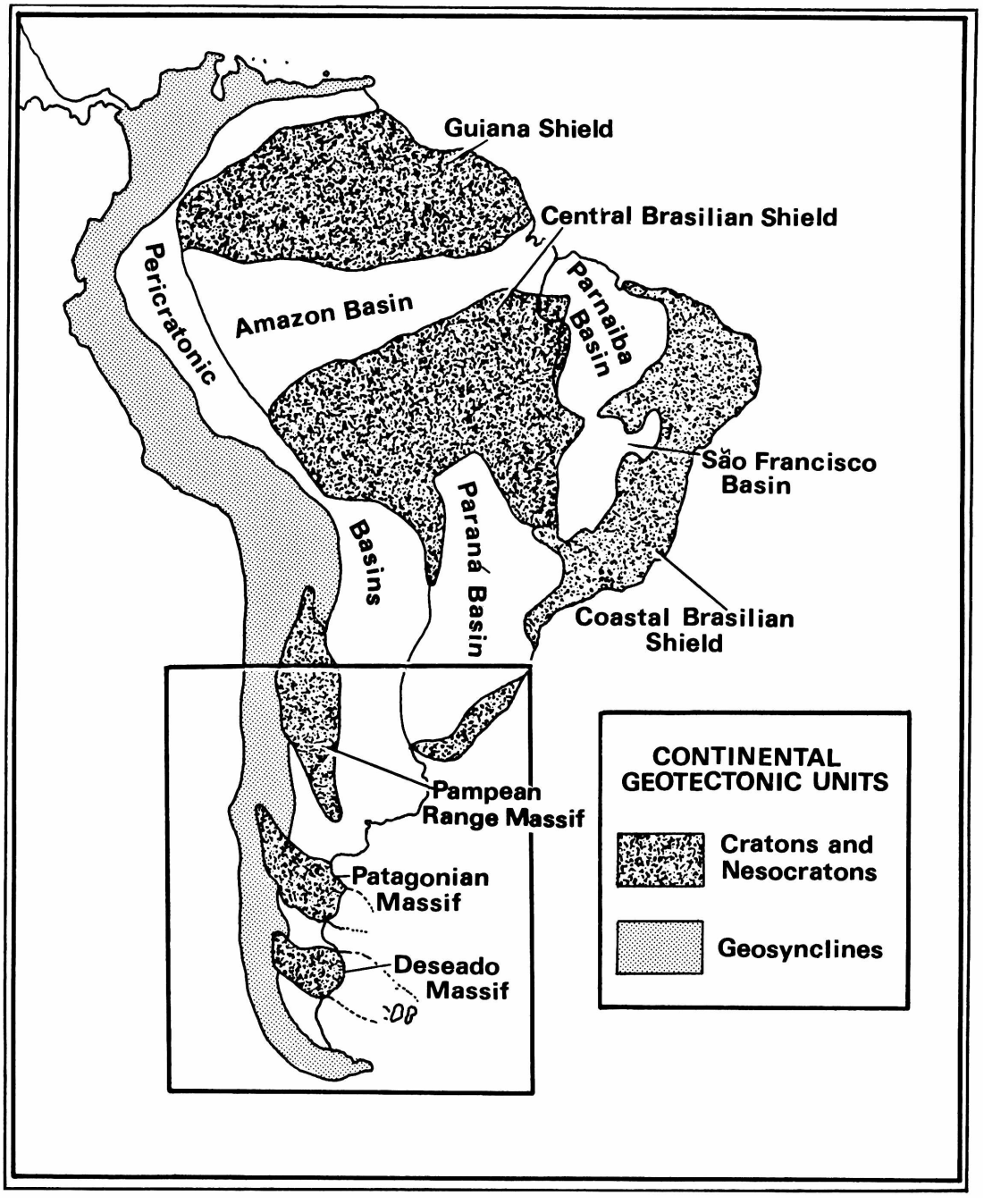

FIG. 13:4. General tectonic structure of South America (after Harrington, 1962). The area in the box is enlarged in figure 5.

Estructura geotectónica de Sud América (según Harrington, 1962). El área en el recorte aparece aumentada en la figura 5.

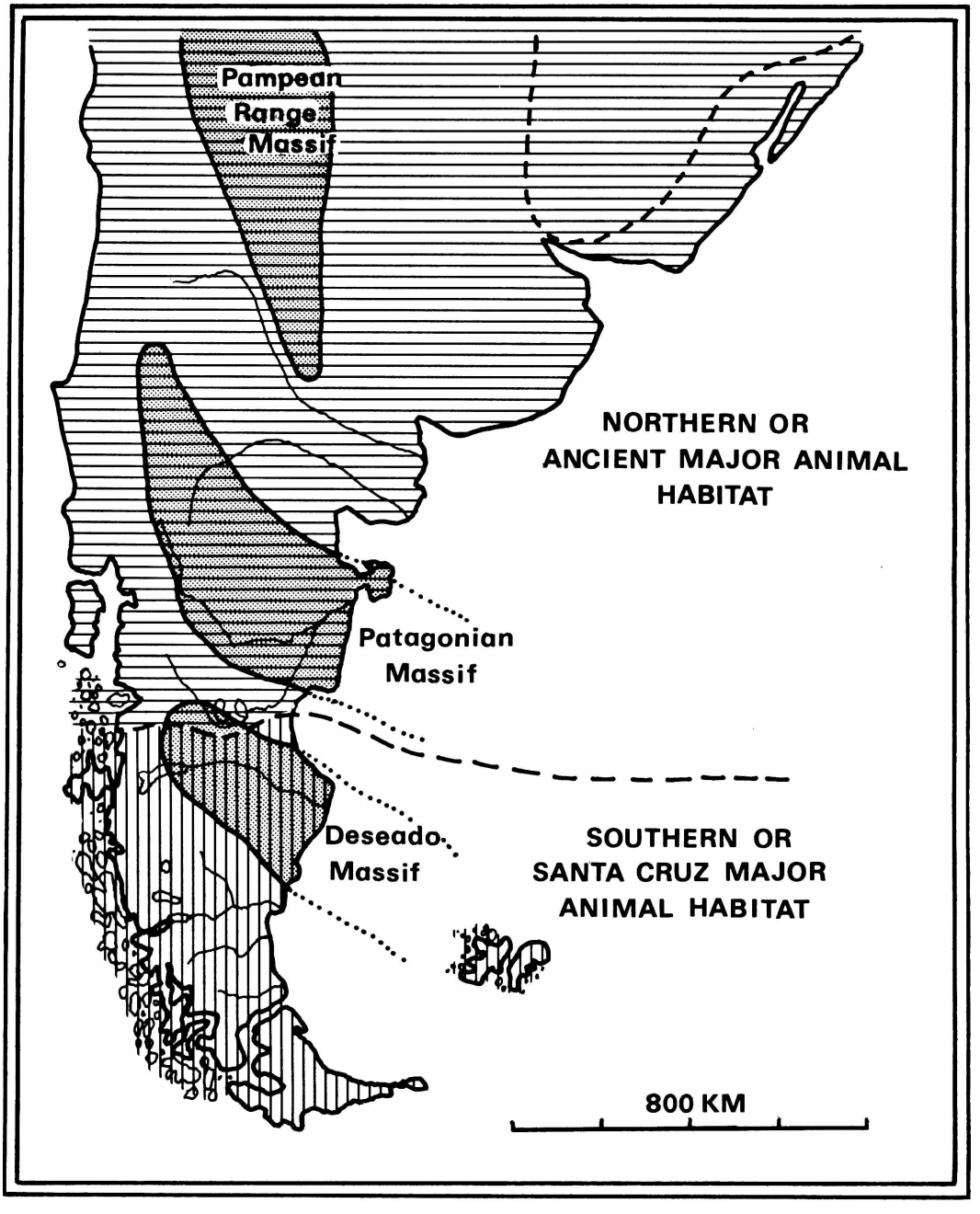

FIG. 13:5. Location of the southern massifs and their relation to the major Patagonian herpetofaunal regions.

Ubicación de los macizos australes y su relación con las regiones herpetofaunísticas fundamentales patagónicas.

tion) and the Meseta de Canquel, plus smaller mesetas of the same lower and middle Tertiary age along the Andean front; their small lakes are close to the last eastern patches of *Nothofagus* and *Araucaria* forests. Along the base of the Andes there is an Austral-Patagonian ecotonal zone; however, it is much narrower than the Monte-Patagonian ecotone extending from the Río Colorado to Valcheta, onto the northern spurs of the Meseta de Somuncurá, and southward to near Bahia Camarones on the Atlantic coast (Cabrera, 1951).

Floristically, the ancient Patagonian region is characterized by a predominantly steppe vegetation with scattered green bushes (*Mulinum spinosum*), several grasses, low herbaceous plants, some spiny plants, and a variety of low bushes; additional kinds of plants are present in saline environments and riparian situations (Table 13:1). The most characteristic element of the monte formations is the creosote bush (*Larrea*), which is represented by five sympatric species in the ecotonal zone at Valcheta (Río Negro). In typical Patagonian landscapes only the low *Larrea ameghinoi* is present.

The cool Patagonian steppes dominated by *Mulinum* and *Stipa*, with scattered creeping, cushionlike plants, exist in western Neuquén, southwestern Río Negro, and in most of Chubut, provinces. In these areas the steppes are commonly associated with basaltic landscapes resulting from the rampant Cenozoic volcanic activity. The steppes are discontinuous in northern Neuquén and Río Negro provinces, where they occur mostly at elevations of more than 900 to 1000 m.

The southern or Santa Cruz Faunal Region extends from about 45°S to the Straits of Magellan (Fig. 13:7). This region encompasses some distinct physiographic areas. The arid valley of the Río Deseado borders the northern limits of the large Altiplanicie Central, a dead volcanic landscape with scattered clay basins and petrified early Cenozoic trees (*Auracarites*). South of the great plateau the drainage basins of the ríos Chalia, Santa Cruz, Coyle, and Gallegos provide more moist lowlands extending to the Straits of Magellan. These rivers drain the glacial valleys of the rugged southernmost Andean cordillera. The Andes are commonly bordered by sharp-edged basaltic mesetas having elevations of 1000 to 1500 m.

TABLE 13:1.—Characteristic Types of Vegetation in the Ancient Patagonian Region.

Herbs	**Spiny or Sclerotic Plants**
Stipa	*Chuquiraga*
Festuca	*Nassauvia*
Poa	*Ephedra*
Senecio filaginoides	*Styllingia*
Grindelia chiloensis	*Verbena*
Verbena ligustrina	*Pantacantha*
Acaena caespitosa	*Adesmia*
Shrubs	*Austrocactus*
Mulinum spinosum	**Hydrophyllic Plants**
Colliguaja integerrima	*Juncus*
Berberis cuneata	*Carex*
Lycium tenuispinosum	*Ranunculus*
Anarthrophyllum rigidum	*Hypsela*
Anarthrophyllum desideratum	*Plagiobothrys*
	Acaena macrostemon
Trevoa spinifer	*Caltha*
Prosopis patagonica	*Cortaderia*
Larrea ameghinoi	*Azorella*
Halophyllic Plants	
Atriplex	
Frankenia	
Spartina	

Phytogeographically, the Santa Cruz Faunal Region agrees with Cabrera's (1951) Patagonian districts—Patagonico Subandino, Patagonico Central, and Golfo de San Jorge. The Patagonico Subandino includes the basaltic mesetas (e.g., Meseta Vizcachas, Meseta Asador, Meseta de la Muerte, and the Meseta de Lago del Sello) and the southern humid lowlands.[1] In these areas open steppe associations of *Festuca monticola, Bromus macranthus, Hordeum comosum, Agropyron magellanicum, Poa* sp., and *Deschampsia* sp. predominate, but some shrubs (*Berberis cuneata, Nassauvia aculeata,* or *Mulinum spinosum*) are present.

Phytogeographic differences between the Sub-Andean district and the central and San Jorge districts are evident by the monotonous grasslands of *Stipa humilis* in the latter. The grasses are interrupted by the broad circular bushes of the blackish "mata negra" (*Verbena*

[1] Although the Sub-Andean District is considered to be a single physiographic unit (Fig. 13:7), for purposes of herpetofaunal analysis, I distinguish the Humid Southern Lowlands.

TABLE 13:2.—Comparison of the Herpetofaunas in Ten Districts in Patagonia. (Numbers of species is a given district are in boldface; numbers of species in common to two districts are in Roman, and the italics are Faunal Resemblance Factors [$N_1 + N_2 / 2C$ (Duellman, 1966)].

	Monte	Monte-Patagonian Ecotone	Patagonian Steppe	Volcanic Highlands	Meseta de Somuncurá	Altiplano Central	Coastal District	Humid Southern Lowlands	Sub-Andean Area	Meseta del Lago de Sello
Monte	**17**	17	2	3	--	1	1	--	--	--
Monte-Patagonian Ecotone	*0.69*	**32**	7	7	4	5	4	2	1	--
Patagonian Steppe	*0.12*	*0.29*	**17**	12	7	8	7	3	3	--
Volcanic Highlands	*0.14*	*0.25*	*0.57*	**25**	8	6	5	3	1	--
Meseta de Somuncurá	.....	*0.19*	*0.50*	*0.44*	**11**	5	4	2	1	--
Altiplanicie Central	*0.08*	*0.24*	*0.62*	*0.35*	*0.50*	**9**	8	3	4	--
Coastal District	*0.08*	*0.20*	*0.56*	*0.30*	*0.42*	*0.94*	**8**	2	4	--
Humid Southern Lowlands	.....	*0.11*	*0.26*	*0.19*	*0.24*	*0.40*	*0.29*	**6**	1	2
Sub-Andean Area	.....	*0.06*	*0.29*	*0.07*	*0.13*	*0.62*	*0.67*	*0.20*	**4**	--
Meseta del Lago de Sello	.....	.....	.....	.....	.....	.....	.....	*0.44*	.....	**3**

tridens). Where shrubby formations occur, dominant plants are *Prosopis patagonica, Lycium ameghinoi, Berberis cuneata, Chuquiraga aurea* and *avellanedae, Brachyclados caespitosus, Acantholippia seriphioides, Pleurofora patagonica, Ameghinoa* sp., and *Euphorbia* sp. The small trees, *Trevoa patagonica*, around the Golfo de San Jorge and in the arid valley of the Río Deseado are the most conspicuous plants in the southern region.

COMPOSITION OF THE HERPETOFAUNA

The herpetofauna of the Patagonian steppe is composed of 60 species, six of which have two or more subspecies in Patagonia; the entire herpetofauna consists of 70 species and subspecies with a noticeable degree of endemism. The fauna is made up of 14 species of anurans (23.3%), one turtle (1.7%), 34 lizards (56.7%), and 11 snakes (18.3%). For purposes of discussion, the herpetofauna has been divided according to the two major faunal regions. Of the 60 Patagonian species, 56 occur in the northern or ancient Patagonian Region, and 13 occur in the southern or Santa Cruz Region; nine species are common to the two regions (Table 13:2, Appendix 13:1). Although lizards are dominant in both regions, they comprise a much higher percentage of the herpetofauna in the southern region (Fig. 13:8).

Northern Patagonian Herpetofauna

For purposes of analysis, the region has been divided into five ecophysiographic areas (Fig. 13:6)—1) Monte associations, 2) Monte-Patagonian ecotone, 3) Patagonian steppe, 4) Volcanic highlands, and 5) Meseta de Somuncurá. The distributions of the species and subspecies of amphibians and reptiles in these five areas are tabulated in Appendix 13:1. The sole Patagonian turtle, *Geochelone donosobarrosi*, and all of the Patagonian anurans are in the northern region, although one species, *Pleurodema bufonina*, is widely distributed in the southern region. Likewise, the single amphisbaenian and all of the snakes are in the northern region, although *Bothrops ammodytoides* enters the southern region.

All of the 17 species occurring in the monte associations are among the 32 species in the Monte-Patagonian ecotone. Included in these areas are several species characteristic of, or related to species in, the more northern regions—Pampas and Chaco; this is true of

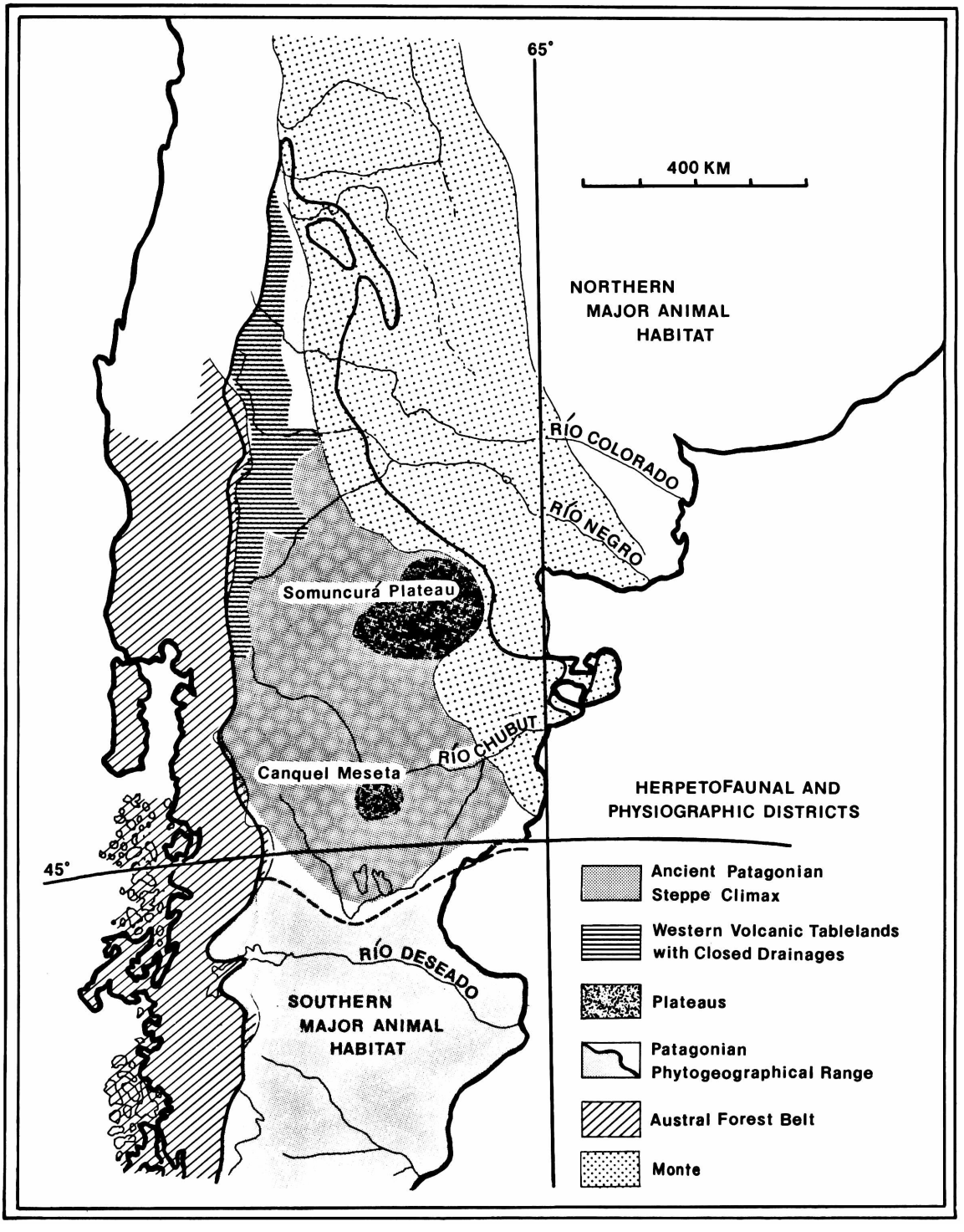

FIG. 13:6. Herpetofaunal and physiographic districts of the ancient Patagonian region.
Distritos herpetofaunísticos y fisiográficos de la región patagónica antigua.

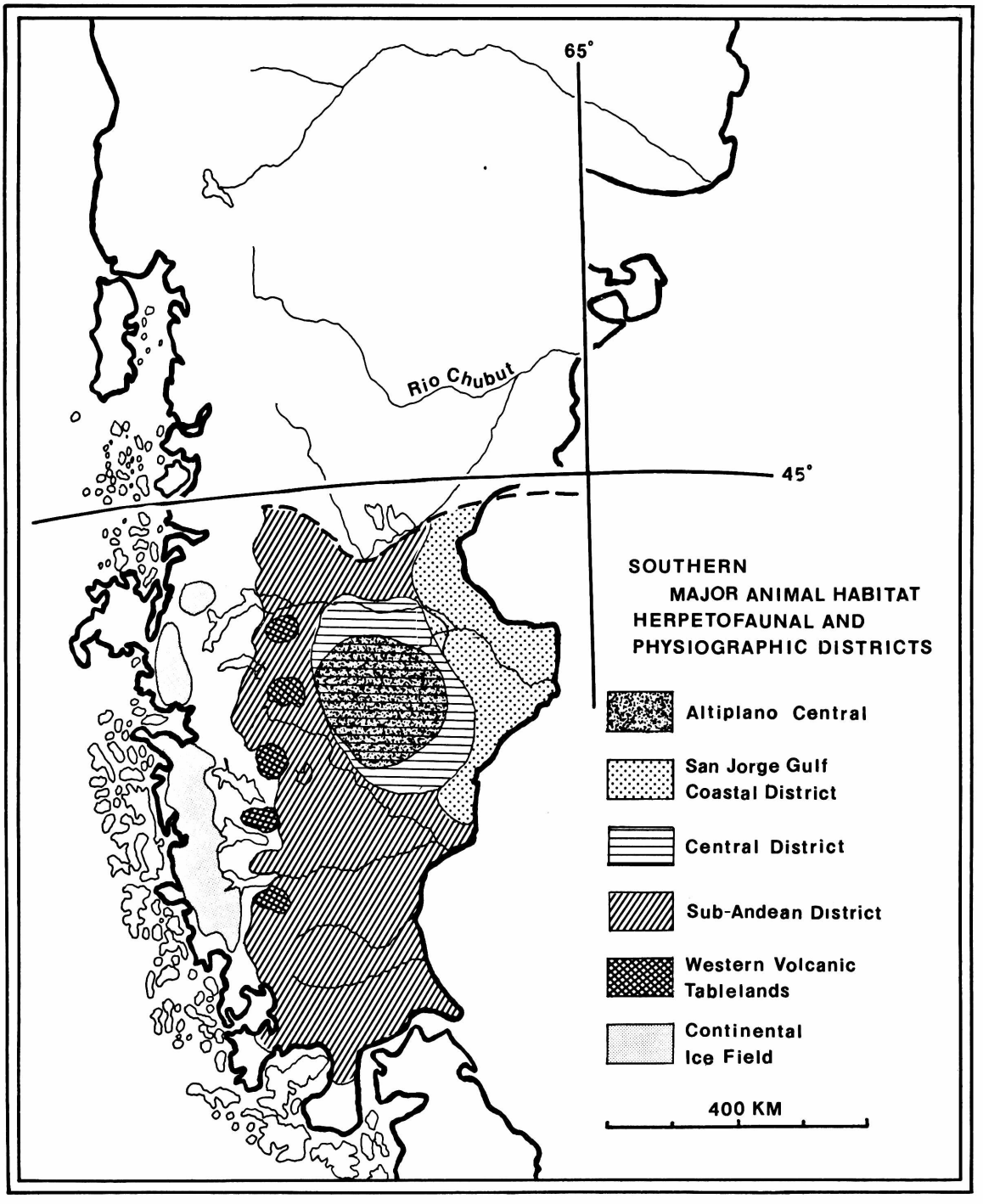

FIG. 13:7. Herpetofaunal and physiographic districts of the southern Patagonian region.
Distritos herpetofaunísticos y fisiográficos de la región sur-patagónica.

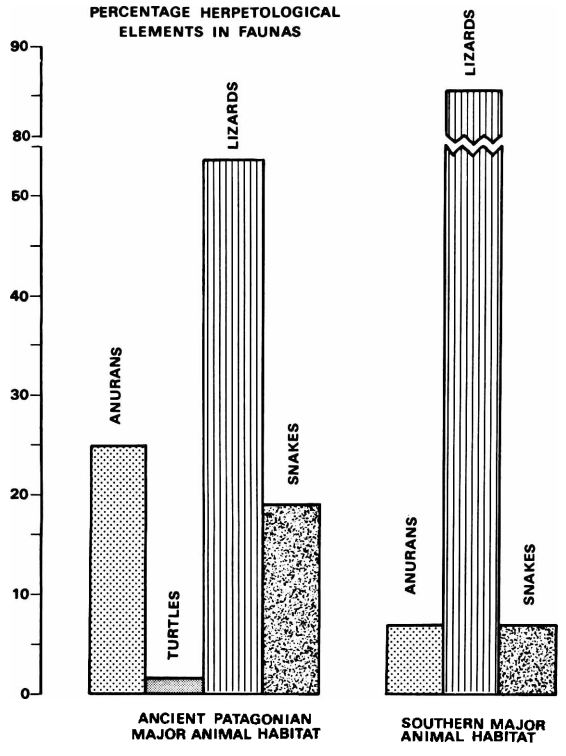

FIG. 13:8. Herpetofaunal composition of the Patagonian regions.

Composición herpetofaunística de las regiones patagónicas.

the anurans *Bufo arenarum* and *Leptodactylus ocellatus*, the lizard *Mabuya frenata*, and the snakes *Elapomorphus bilineatus*, *Lystrophis semicinctus*, and *Micrurus frontalis* (Fig. 13:9). The analysis of latitudinal distributions reveals that *Geochelone donosobarrosi* is a true member of the xerophytic scrub association south of the Río Colorado and only slightly penetrates the neighboring flats of the Pampean region. The distributions of the snake *Philodryas patagoniensis* and the lizard *Proctotretus pectinatus* extend eastward into the Pampean region (Figs. 13:10–11). On the contrary, the frog *Pleurodema bufonina* and the lizards *Homonota darwinii* and *Liolaemus bibronii* are characteristic Patagonian elements and only enter the monte peripherally; these species ascend the Andean slopes north of the Río Barrancas.

In the Patagonian steppes, extrusive basaltic rocks provide shelter for numerous lizards. *Liolaemus elongatus* is a conspicuous species in rocky areas, some of which also are inhabited by more cryptic lizards—*Liolaemus ceii* and *L. kriegi*. Isolated populations of *Phymaturus patagonicus* are subspecifically distinct—*P. p. patagonicus* in the valley of the Río Chubut and *P. p. indistinctus* in the Sierra de San Bernardo (Cei and Castro, 1973) (Fig. 13:12). *Liolaemus fitzingeri canqueli* inhabits the rocky slopes of the Meseta de Canquel and extends eastward through the salt flats to the coast, where it meets *L. f. fitzingeri*, the subspecies that is common in southern Chubut and Santa Cruz. *Diplolaemus bibronii*, more characteristic of the southern region, reaches the northern limits of its distribution at the edge of the Meseta de Somuncurá (Cei, 1971b).

Clay soils in the region hold water in the form of temporary ponds during the brief rainy season. These ponds and intermittent and permanent streams are the habitats and/or breeding sites for several species of anurans, especially leptodactylids (Barrio, 1973; Cei, 1969a,b, 1970b, 1972b; Cei and Roig, 1966, 1968; Gallardo, 1970). Some species have restricted ranges; for example, *Atelognathus solitarius* is known only from Arroyo Las Bayas, south of Pilcaniyeu, Río Negro.

Twenty-four species are known to inhabit the volcanic plateaus and extra-Andean highlands in western Neuquén and Río Negro provinces. Among them are four species of telmatobiine leptodactylid frogs (Fig. 13:3). The aquatic *Atelognathus patagonicus* is confined to the Laguna Blanca Basin. The semiterrestrial *Atelognathus praebasalticus* is composed of four geographically isolated subspecies—*A. p. praebasalticus* at Laguna Blanca, *A. p. agilis* at Laguna Casa de Piedra, *A. p. luisi* at Laguna Catan Lil, and *A. p. dobeslawi* at Barda de Santo Tomas (Cei, 1972b). *Atelognathus nitoi* and *Alsodes gargola gargola* have different distributional traits. In western Río Negro these frogs occur in small Andean lakes—Laguna Verde near Cerro Blanco at about 1450 m elevation (Barrio, 1973), and Laguna Tonchek and Laguna Schmoll at 1700 to 1750 m on the slopes of Cerro Catedral near Bariloche (Gallardo, 1970). Together with *Alsodes gargola*

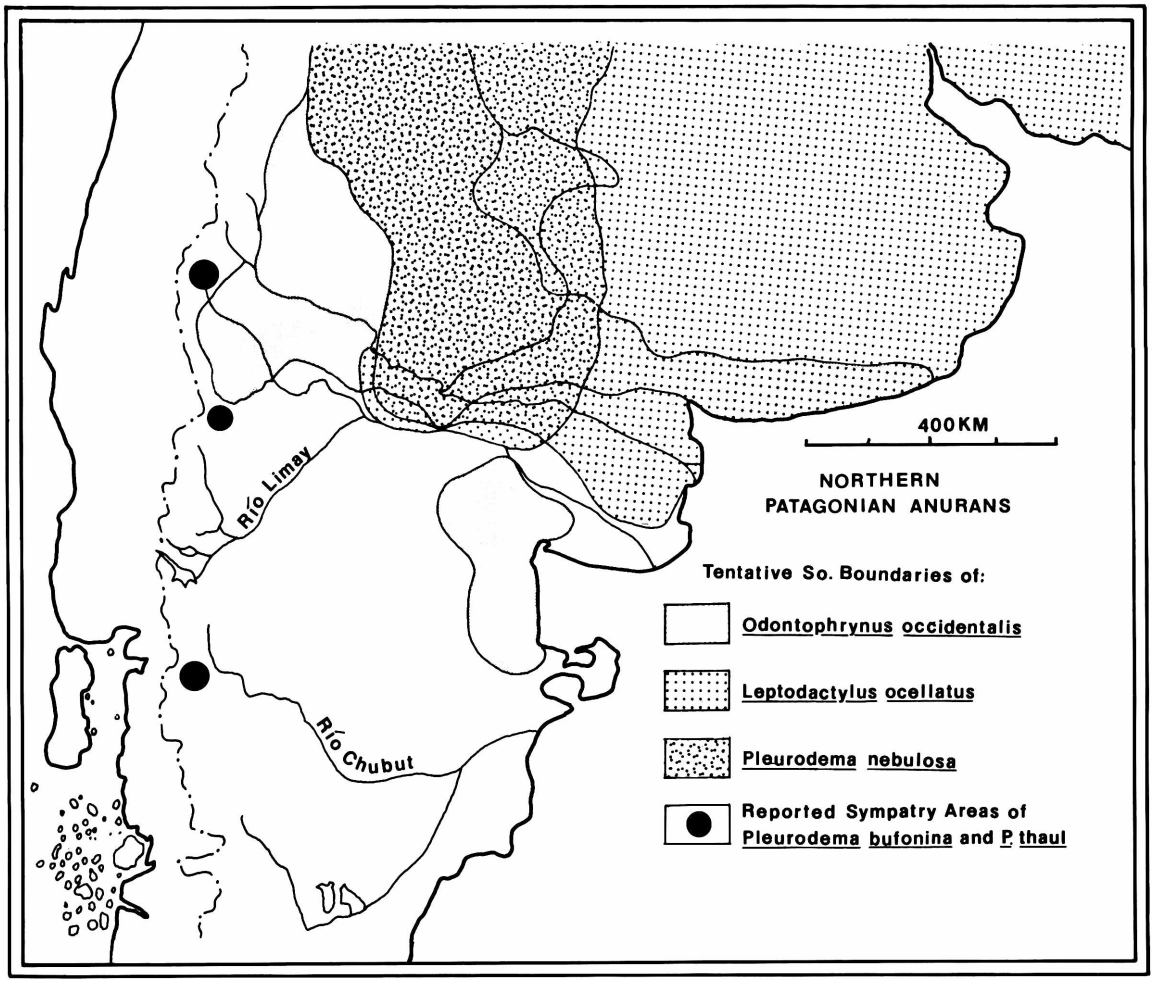

FIG. 13:9. Southern limits of distribution of taxa in the monte formation in northern Patagonia. Areas of sympatry of *Pleurodema bufonina* and *P. thaul* are indicated.

Límites meridionales de distribución de taxa en la formación del monte en el norte patagónico. Se indica las áreas de simpatría de Pleurodema bufonina *y* P. thaul.

neuquensis from the thermal brooks on the sandy Meseta Lonco Luan, 1500 m elevation in Neuquén (Cei, 1976), they belong to a transitional herpetofauna of the austral-Patagonian ecotone. Other transitional species are the frog *Pleurodema thaul* and two lizards, *Liolaemus tenuis* and *Diplolaemus leopardinus*, all characteristic inhabitants of *Araucaria* forests (Cei, 1970a, 1974b). On the xeric Meseta de Lonco Luán, dead patches of *Nothofagus* and *Chusquea* exist near the border of the *Araucaria* forests. *Liolaemus lineomaculatus* occurs on the Meseta de Lonco Luán. In other ecotonal and subandean areas of Neuquén, *Pleurodema thaul*, *Liolaemus chilensis*, and *L. buergeri* are found. The latter occurs sympatrically with the typical Patagonian lizards *Liolaemus elongatus* and *L. kriegi*. Likewise, the characteristic lizards of rocky Patagonian communities, *Phymaturus palluma* and *P. patagonicus zapalensis* occur on the basaltic plateaus. *Phymaturus palluma* extends northward in the Andes at elevations of 3000 to 3500 m to La Rioja and San Juan, and *P. patagonicus* has distinct populations (*P. p. payuniae* and *P. p. nevadoi*) to the

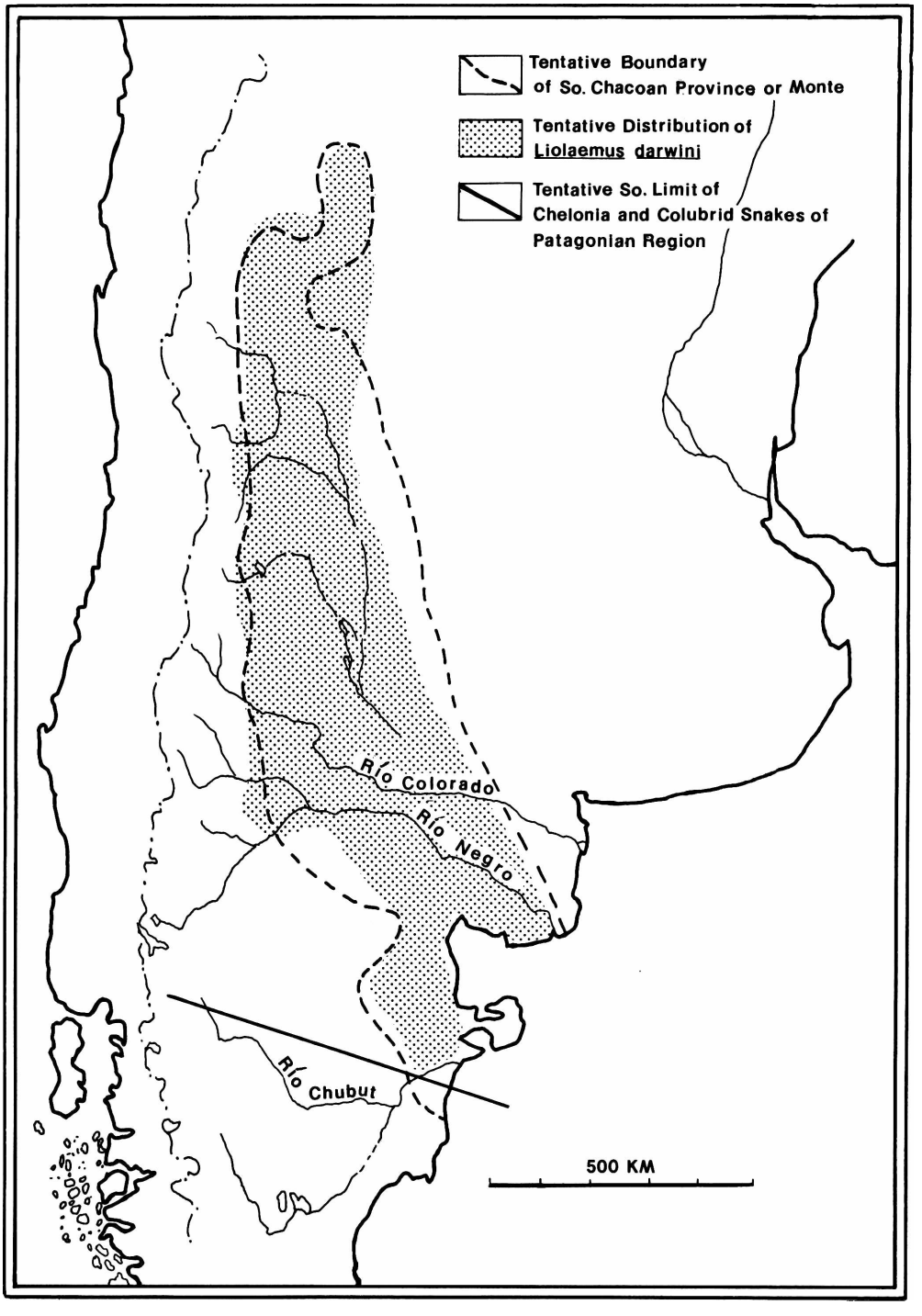

FIG. 13:10. Distribution of *Liolaemus darwinii*, a characteristic species of the monte formation. The southern edge of this formation is the southern limits of distribution of *Geochelone* and of colubrid snakes in northern Patagonia.

Distribución de Liolaemus darwinii, *especie caracteristica de la formación del monte. El límite meridional de esta formación es el límite meridional de* Geochelone *y de los ofidios colúbridos en la Patagonia septentrional.*

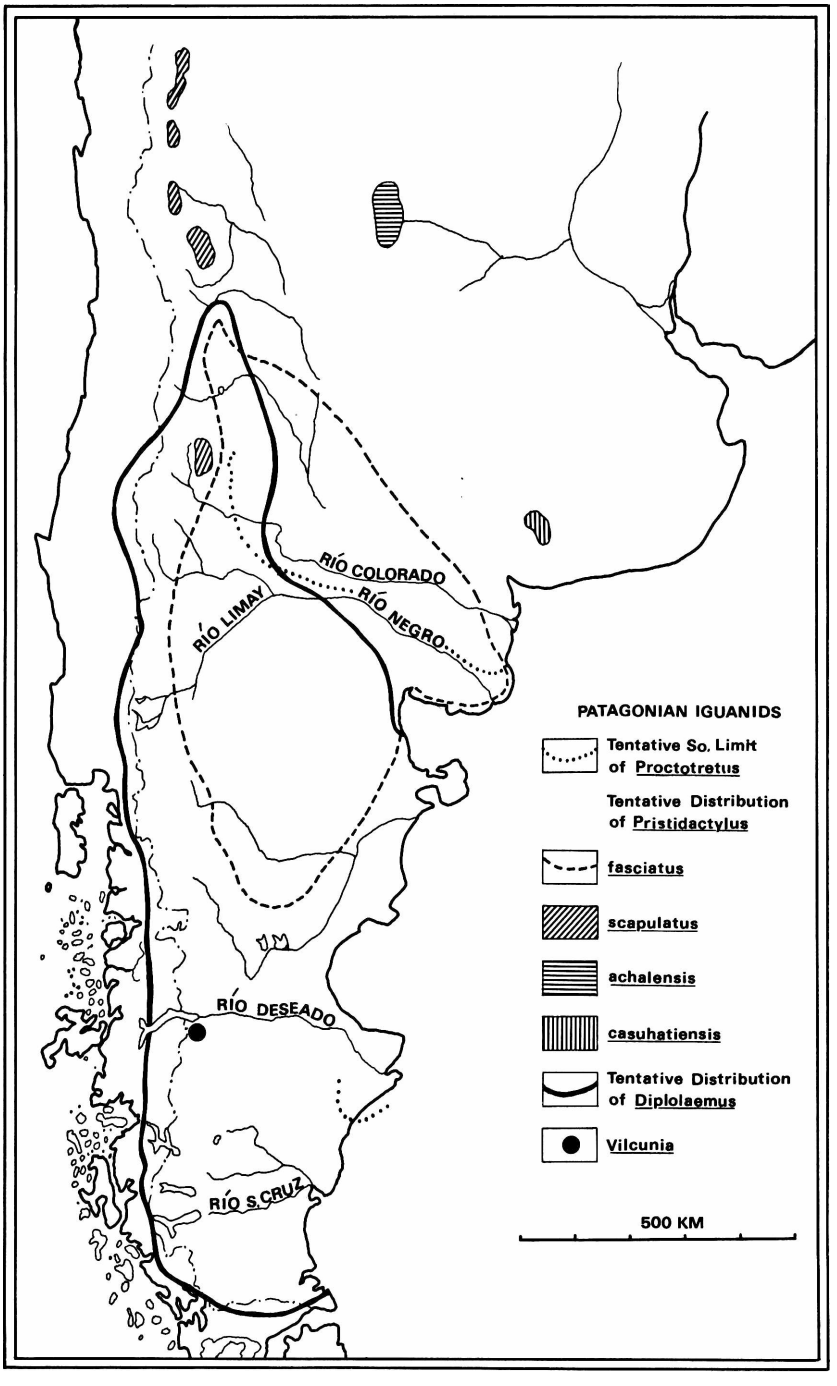

FIG. 13:11. Patterns of distribution of tropidurine iguanid lizards in Patagonia.
Distribución de los saurios iguánidos tropidurinos en Patagonia.

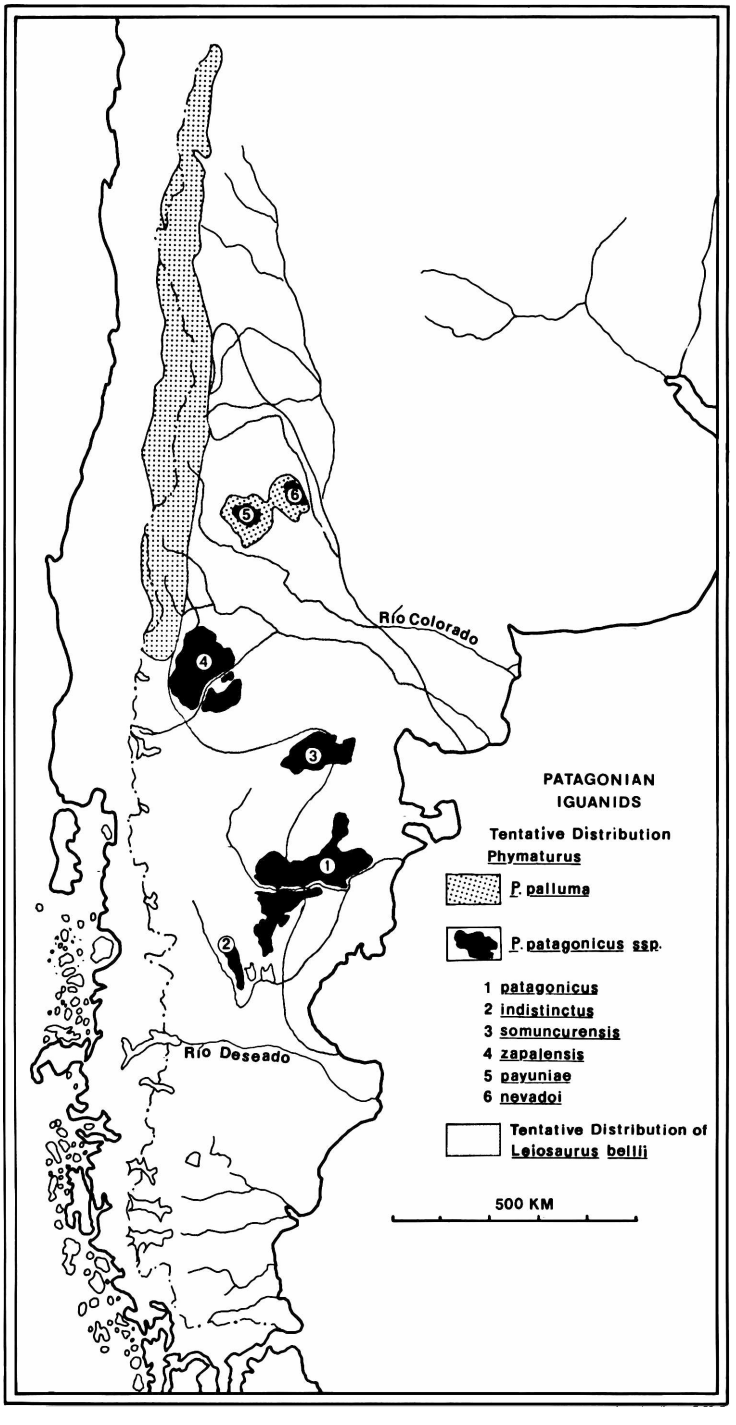

FIG. 13:12. Patterns of distribution of tropidurine iguanid lizards in Patagonia.
Distribución de los saurios iguánidos tropidurinos en Patagonia.

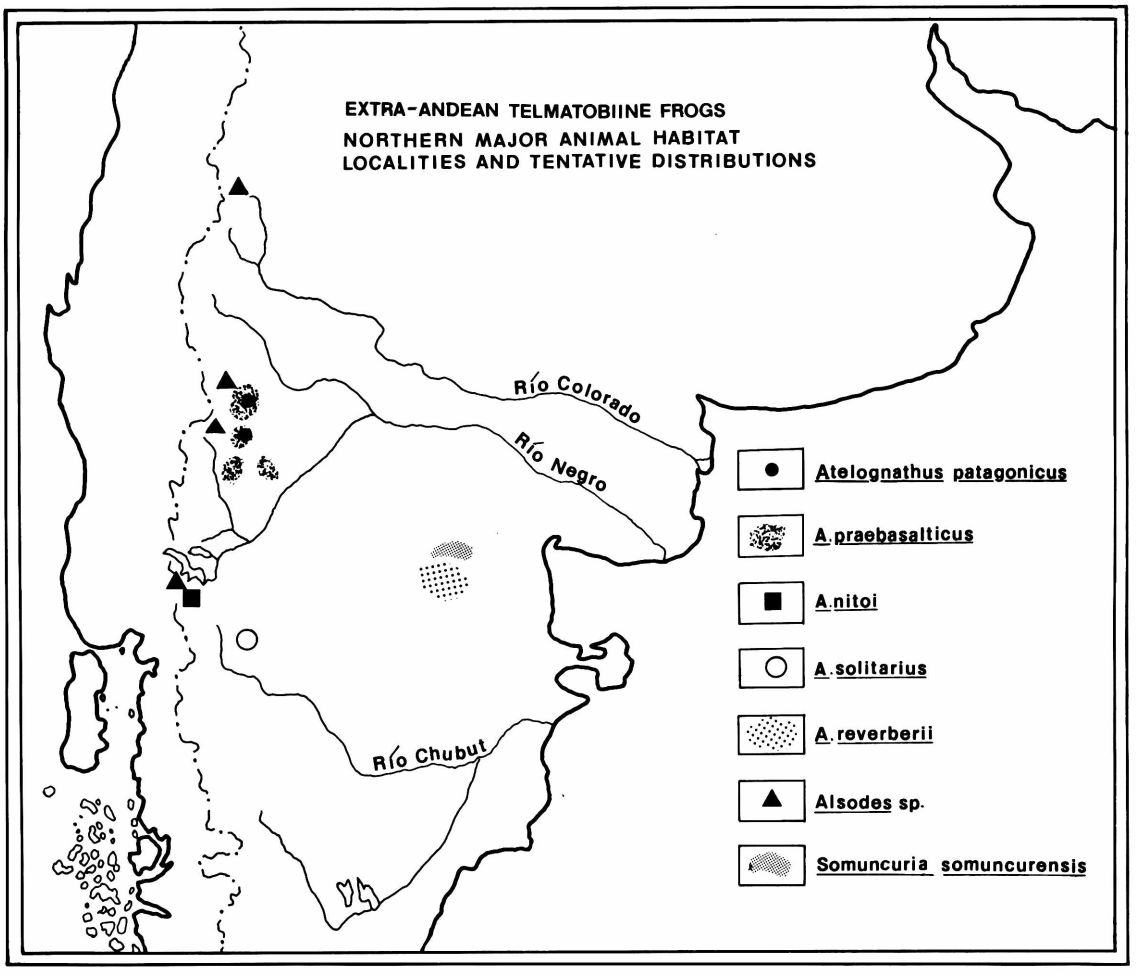

FIG. 13:13. Distribution of extra-Andean telmatobiine frogs in northern Patagonia.
Distribución de los anuros telmatobiinos extra-andinos en la Patagonia septentrional.

north in southern Mendoza Province (Cei and Castro, 1973; Cei and Roig, 1975) (Fig. 13:12).

The isolated Meseta de Somuncurá (150 × 80 km), with elevations to 1700 m, has some peculiar habitats. Between 800 and 1700 m, above the Monte-Patagonian ecotone, 11 species of amphibians and reptiles are known. Six of the species are widespread in Patagonia—*Pleurodema bufonina, Homonota darwinii, Diplolaemus darwinii, Liolaemus bibronii, L. boulengeri*, and *L. rothi.* Three other species and two subspecies are endemic —*Phymaturus patagonicus somuncurensis* and *Liolaemus elongatus petrophilus* are the endemic subspecies of lizards. The endemic *Liolaemus ruizleali* inhabits rocky summits of the meseta at 1200 to 1700 m. The two endemic, telmatobiine leptodactylid frogs have unique morphological and ecological traits. The monotypic *Somuncuria somuncurensis* lives in streams at 800 to 1000 m issuing from thermal springs on the northeastern slopes of the meseta. Inhabiting the same streams having a temperature of about 18°C is the endemic characid fish *Gymnochacinus bergi.* Conversely, *Atelognathus reverberii*, a nearly fossorial frog, inhabits the arid plateau at elevations of more than 1000 m and breeds in small temporary pools.

Southern Patagonian Herpetofauna

The distributions of the 11 lizards, one snake, and one frog are examined with respect to five ecophysiographic areas (Fig. 13:7)—1) Altiplano Central, 2) Coastal District, 3) Humid Southern Lowlands, 4) Sub-Andean Area, and 5) Meseta de Lago del Sello. The distributions of the species and subspecies of amphibians and reptiles in these five areas are tabulated in Appendix 13:1, and the distributional relationships between the areas are analyzed in Table 13:2.

Nine species occur in the Altiplano Central; all but the frog *Pleurodema bufonina* also occur in the coastal district. Only six species occur in the humid southern lowlands; the southernmost frog, *Pleurodema bufonina*, is rather rare there. The lizard *Liolaemus magellanicus*, the only herpetofaunal species on Tierra del Fuego, is common on the southern end of the mainland. Only four species (all lizards) occur in the sub-Andean region.

The Meseta de Lago del Sello at 47°S is nearly 50 km in diameter. On the top of the plateau, low grasses (*Festuca*, *Poa*, and *Stipa*) are dominant with thorny plants or cushion plants (*Benthamiella azorella*, *Verbena*, *Senecio*, *Nassauvia*); lichens are abundant in rocky areas. Owing to the proximity of the great Patagonian Ice Field, cold winds whip the plateau, even in summer. Only three iguanid lizards have been found on the plateau (1200–1600 m); the two species of *Liolaemus* are widespread in southern Patagonia, whereas the monotypic *Vilcunia sylvanae* is endemic. No amphibians have been found on the plateau; the widespread *Pleurodema bufonina* ascends the slopes to only 900 m.

ORIGIN OF THE HERPETOFAUNA

The Patagonian herpetofauna is distinctive in the diversity of telmatobiine leptodactylid frogs and tropidurine iguanid lizards. Most other species inhabiting Patagonia are members of groups that are mainly distributed to the north of Patagonia. Thus, *Geochelone*, *Cnemidophorus*, *Mabuya*, *Homonota*, *Leptodactylus*, *Odontophrynus*, *Bufo arenarum*, and all of the genera of snakes are more northern groups.

Bufo spinulosus and *Alsodes* are primarily Andean groups. The former enters Patagonia in many disjunct valleys; the species does not occur on major basaltic mesetas. In Patagonia, *Alsodes* occurs only in the volcanic highlands adjacent to the Andes.

Pleurodema is a primitive leptodactyline that may have originated in, and dispersed from, the austral forests (Duellman and Veloso, 1977); the genus has dispersed northward in nonforested habitats to the Caribbean. Two species are peripheral in Patagonia—*P. thaul* in the austral forest—Patagonian steppe ecotone and *P. nebulosa* in the monte. *Pleurodema bufonina* is a widespread species endemic to Patagonian habitats. Although *P. thaul* and *bufonina* are distinctive in their morphology and behavior, populations intermediate between the species exist in high valleys in western Neuquén.

Lynch (1978) provided an hypothesis for the evolution of lower telmatobiine frogs in Patagonia. The peculiar monotypic *Somuncuria* is endemic to the Meseta de Somuncurá, whereas five species of *Atelognathus* occur in isolated basaltic areas in Patagonia. The only extra-Patagonian *Atelognathus* is *A. grandisonae* from Puerto Eden in extreme southern Chile.

Among the iguanid lizards, the monotypic *Vilcunia* has characters of both *Proctotretus* and *Liolaemus* and is endemic to southern Patagonia (Donoso Barros and Cei, 1971). *Diplolaemus* and *Phymaturus* are fundamentally austral genera (Figs. 13:11–12). *Ctenoblepharis*, *Leiosaurus*, *Proctotretus*, and *Pristidactylus* are widely distributed to the north of Patagonia (Cei, 1973c,d). Two species of *Proctotretus* are distributed in temperate areas in southern Brasil, Uruguay, and central Argentina; *P. pectinatus* occurs in the monte-Patagonian ecotone. *Pristidactylus fasciatus* is primarily Patagonian, but congeners occur in disjunct Andean areas (*P. scapulatus*) and in isolated extra-Andean massifs of central Argentina—Sierra Grande de Córdoba (*P. achalensis*) and Sierra de la Ventana (*P. casuhatiensis*) (Gallardo, 1964, 1968; Cei and Castro, 1975).

Three major points relative to the origin and evolution of the Patagonian herpetofauna need to be emphasized.

1. There has been a radiation of primitive leptodactylid frogs, remnants of Gondwanan elements. Vuilleumier (1968) and Lynch (1971, 1978) noted the austral center of radiation of telmatobiine leptodactylids in Patagonia and the austral forests; Formas (this volume) discussed the biogeography and ecology of the telmatobiines of the austral forests—*Alsodes, Batrachyla, Caudiverbera, Eupsophus, Hylorina, Insuetophrynus,* and *Telmatobufo,* some of which also occur in Argentina (Cei, 1978). The limited paleontological evidence supports the austral center of radiation (Schaeffer, 1949; Chaffee, 1952; Casamiquela, 1963; Estes and Reig, 1973).
2. An austral South American center of evolution and adaptive radiation of an ancestral stock of iguanid lizards is evident (Cei, 1973c,d, 1975c; Cei and Castro, 1975). Fourteen genera are austral in Argentina and Chile; seven of these are Patagonian. There are some 20 genera of iguanids in tropical South America and another ten genera in the Sonoran region of North America. With the exception of *Anolis* and *Sceloporus,* no other iguanid genus displays such an impressive adaptive radiation as does *Liolaemus,* the dominant lizards in any Patagonian community. In most of these same communities there exist representatives of the other Patagonian iguanid genera—*Diplolaemus, Leiosaurus, Phymaturus, Pristidactylus, Proctotretus,* and *Vilcunia.*
3. An impressive post-Pleistocene adaptive radiation has taken place in four groups of Patagonian *Liolaemus* (see following section).

Thus, far from being a totally barren region biologically, irregularly colonized by elements from neighboring biotas, Patagonia has been, and apparently still is, a center of active speciation of several herpetofaunal elements. The old radiations are supported by the scattered relicts, unique witnesses to some of the most ancient steps in the history of continental vertebrates, whereas the Recent speciation of *Liolaemus* attests to the continued evolutionary activity in the region.

Evolutionary Radiation of Patagonian Liolaemus

Lizards of the genus *Liolaemus* are widespread in temperate South America. Three species range into southern Brasil, and several species occur in the Andes, two extending northward to central Perú (Duellman, this volume). Twenty-six taxa are Patagonian or Andean-Patagonian.

Four major evolutionary units can be recognized among the Patagonian *Liolaemus* as follows: 1) *L. fitzingeri* complex, 2) *L. elongatus-kriegi* complex, 3) *L. kingii-archeforus* complex, and 4) *L. magellanicus-lineomaculatus* complex (Cei, 1971a, 1972a, 1973a,b 1974a, 1975a,b, 1975d,e; Cei and Scolaro, 1977; Scolaro and Cei, 1977). The lizards that are not members of these groups are primarily peripheral to Patagonia and/or are ecotonal elements. Some of these are members of transcordilleran groups—*Liolaemus altissimus, chilensis, cyanogaster, lemniscatus, pictus,* and *tenuis*; *L. bibronii* is related to the Chilean *L. fuscus. Liolaemus boulengeri, darwinii,* and *gracilis* are members of the more northern monte fauna and are primarily peripheral in Patagonia (Fig. 13:10).

Liolaemus fitzingeri *complex.*—This group is characterized by 1) patch of enlarged scales on posterior surfaces of thighs, especially well developed in males (Fig. 13:14); 2) high number (52–82) of blunt, slightly keeled scales around body; 3) high number (7–11) of preanal pores; 4) stout body and relatively long tail, 1.5 times length of body; 5) tendency to have black venters and dark humeral collars; 6) predominate dorsal color patterns consisting of wide transverse dark blotches, bordered posteriorly by white, but spotted erythristic, and melanistic variations not uncommon.

Content: *L. fitzingeri canqueli, L. fitzingeri fitzingeri, L. fitzingeri melanops, L. rothi,* ?*L. ruizleali. Liolaemus f. fitzingeri* is the

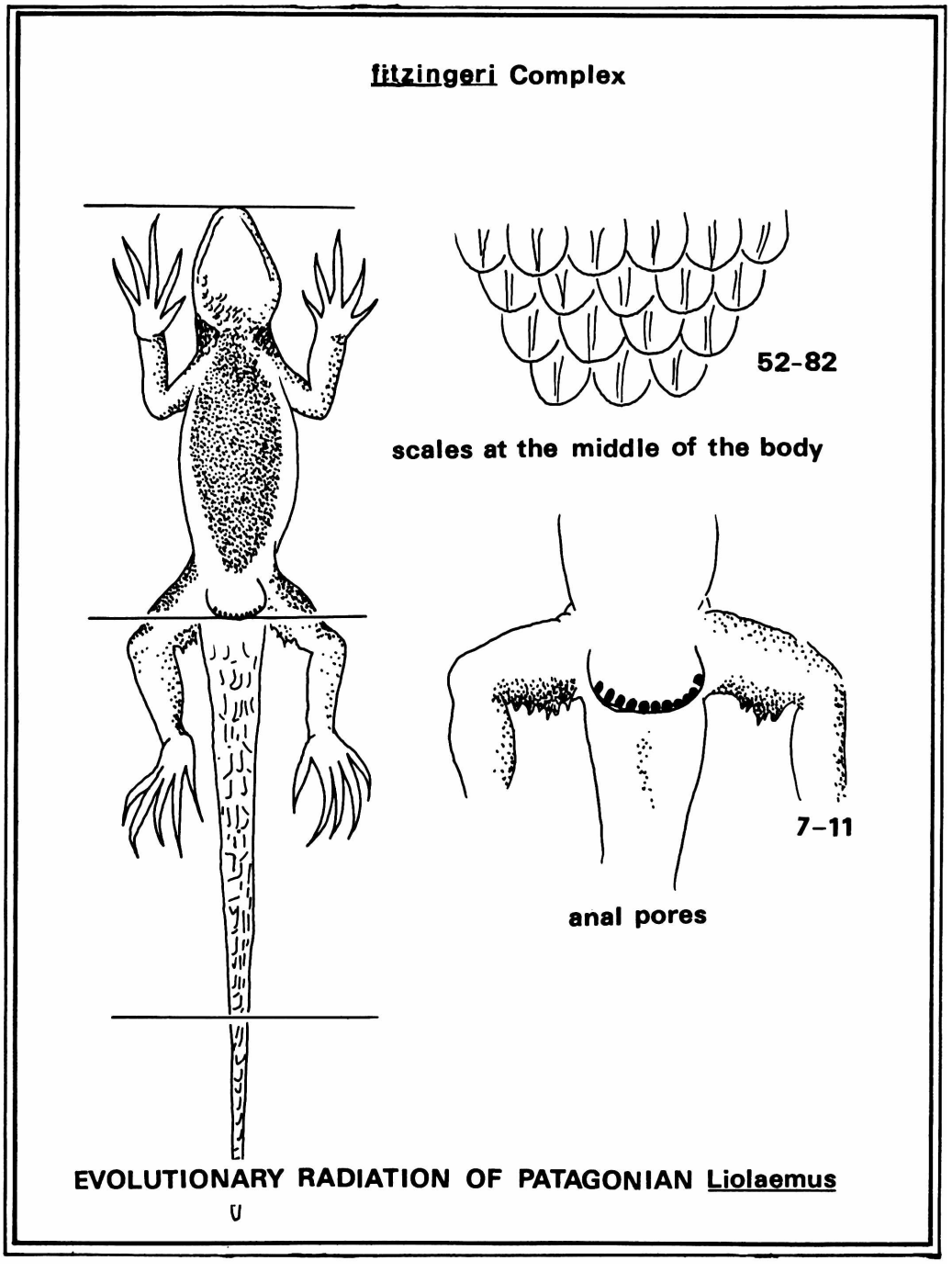

FIG. 13:14. Morphological traits of lizards of the *Liolaemus fitzingeri* complex.
Caracteristicas morfológicas de los saurios del conjunto Liolaemus fitzingeri.

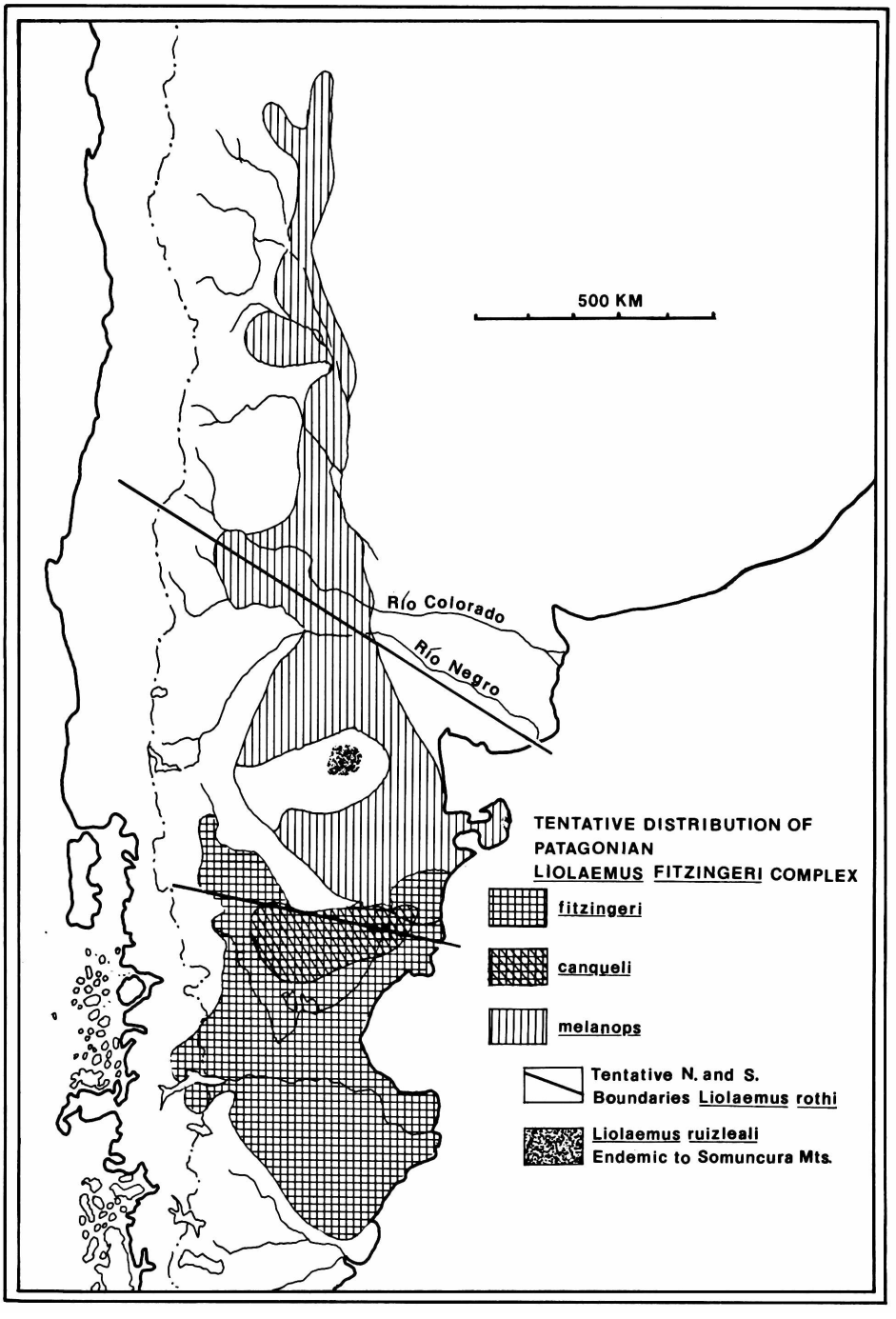

FIG. 13:15. Distribution of the *Liolaemus fitzingeri* complex in Patagonia.
Distribución del conjunto Liolaemus fitzingeri *en Patagonia.*

southernmost member of the group, inhabiting sandy Patagonian steppe in Santa Cruz and Chubut; it meets *L. f. canqueli* in the vicinity of Trelew and Dos Pozos on the coast of Chubut (Cei and Scolaro, 1977). The latter subspecies is characteristic of the arid volcanic massif of Canquel south of the Río Chubut. *Liolaemus f. melanops* is distributed in coastal areas north of the Río Chubut to the Río Negro and thence inland through Mendoza to San Juan and La Rioja. *Liolaemus rothi* is endemic to northern Patagonia, as is *L. ruizleali*, known only from the Meseta de Somuncurá (Fig. 13:15).

Members of the *Liolaemus fitzingeri* complex are mostly stout, polymorphic lizards that are psammophilous or fossorial. The polychromatism in these lizards has been a source of confusion. *Liolaemus melanops* was considered to be a color variety of *L. fitzingeri* by Donoso-Barros (1966) and Peters and Donoso-Barros (1970), and as a northern subspecies of *L. fitzingeri* by Cei (1975d). However, careful analyses of morphological and serological attributes may suggest that *L. melanops* probably is a distinct species. Populations of *L. f. melanops* near Puerto Madryn are highly variable; some individuals are morphologically indistinguishable from *L. goetschi* (Cei, 1975a), a monomorphic lizard extending from the Río Colorado north to San Juan and La Rioja. Serological analysis shows that populations formerly assigned to *L. melanops* and *L. goetschi* are conspecific; thus, only one taxon (*L. melanops*) is recognized (Cei and Scolaro, 1977).

The serological distance between *L. darwinii* and members of the *Liolaemus fitzingeri* complex suggests that *L. darwinii* diverged early from the ancestral stock of that group. Although juveniles and females of *L. darwinii* and *L. boulengeri* are strikingly similar, a noticeable serological distance exists between the species, whereas *L. boulengeri* is serologically closer to *L. f. melanops*.

Liolaemus rothi has morphological characters that ally it with the *Liolaemus fitzingeri* group, but serologically it is not so distant from other Patagonian complexes of *Liolaemus* as are the other members of the *Liolaemus fitzingeri* group. *Liolaemus rothi* could be considered as a primitive, ecologically generalized species of the *Liolaemus fitzingeri* complex. The poorly known *L. ruizleali* is morphologically close to *L. rothi*, except that the postfemoral enlarged scales are absent in *L. ruizleali*.

Enlarged scales on the posterior surfaces of the thighs are characteristic of some other extra-Patagonian *Liolaemus*. Such is the case in the Andean *L. ornatus* and *L. mocquardi*, which morphologically are similar to *L. darwinii*. The character also is present in *L. wiegmannii* in southeastern Brasil, Uruguay, and the Argentine pampas, and in *L. multimaculatus* from the Atlantic coast of Buenos Aires. Because of the many differences displayed by these two lizards from one another and from members of the *Liolaemus fitzingeri* complex, the enlarged postfemoral scales are considered to be independently evolved characters in these three lines.

Liolaemus elongatus–kriegi *complex*.—This group is characterized by 1) no patch of enlarged scales, but a row of projecting scales on posterior surface of thigh; 2) high number (72–120) of acuminate, keeled scales around body (Fig. 13:16); 3) few (1–4) preanal pores; 4) slender body with very long tail; 5) absence of ventral melanism and dark nuchal collar; 6) dorsal pattern of blackish irregular stripes, not bordered by white, and confluent into vertebral and lateral bands.

Content: *L. austromendocinus, L. buergeri, L. ceii, L. elongatus elongatus, L. elongatus petrophilus, L. kriegi. Liolaemus elongatus* is widespread in rocky habitats in Chubut, Río Negro, and Neuquén, and northward in the precordillera in Mendoza (Fig. 13:17). It is a highly variable species, and notable serological distances have been found among scattered, isolated populations (Cei, 1974a); only the population of the Meseta de Somuncurá has been recognized taxonomically—*L. e. petrophilus. Liolaemus austromendocinus* occurs in arid habitats below 1500 m in volcanic regions in southern Mendoza and in the Río Neuquén and Río Colorado basins. *Liolaemus kriegi* occupies basaltic areas in Neuquén and Río Negro, where it occurs sympatrically with *L. ceii. Liolaemus buergeri* occurs sympatrically with *L.*

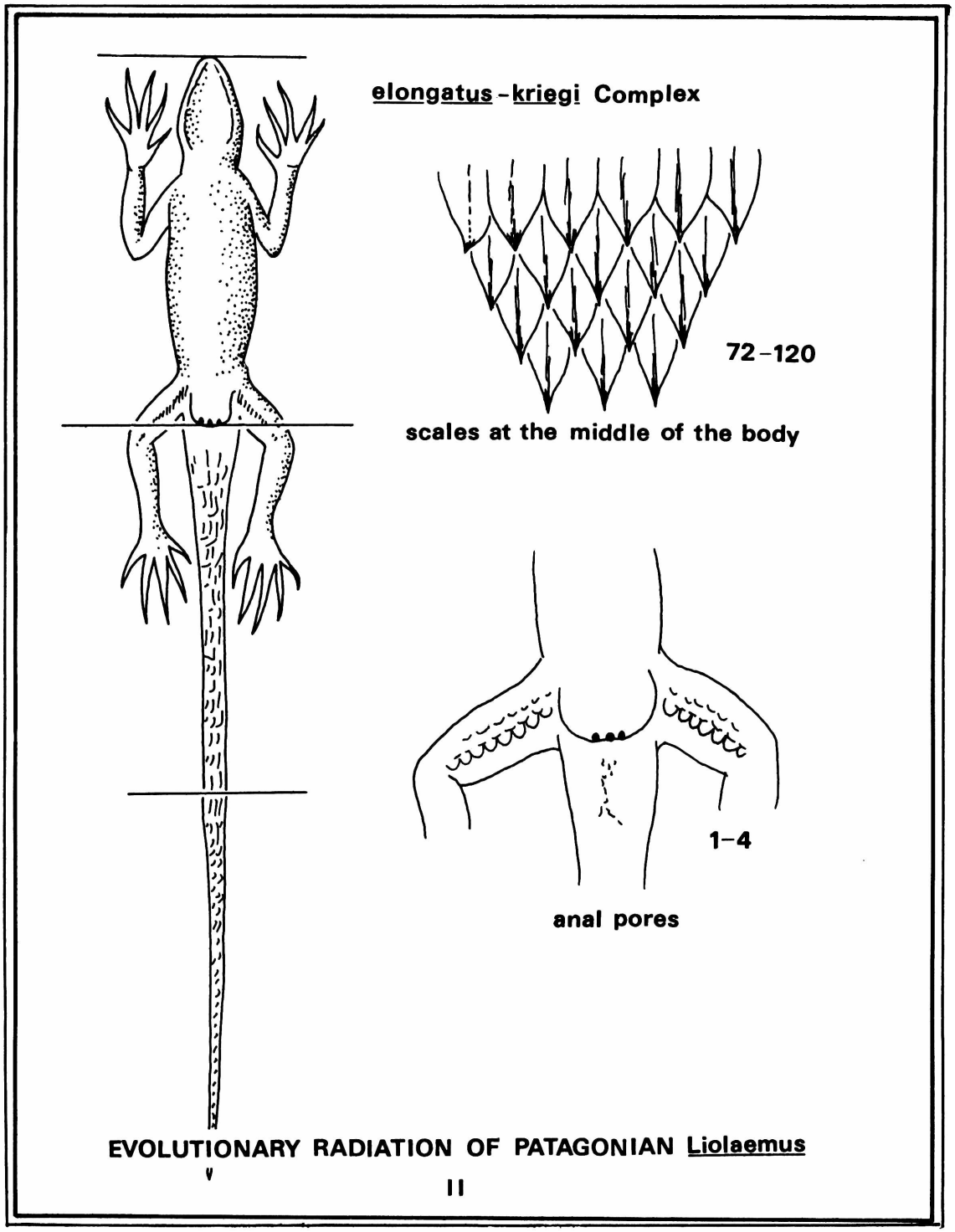

FIG. 13:16. Morphological traits of lizards of the *Liolaemus elongatus-kriegi* complex. *Caracteristicas morfológicas de los saurios del conjunto* Liolaemus elongatus-kriegi.

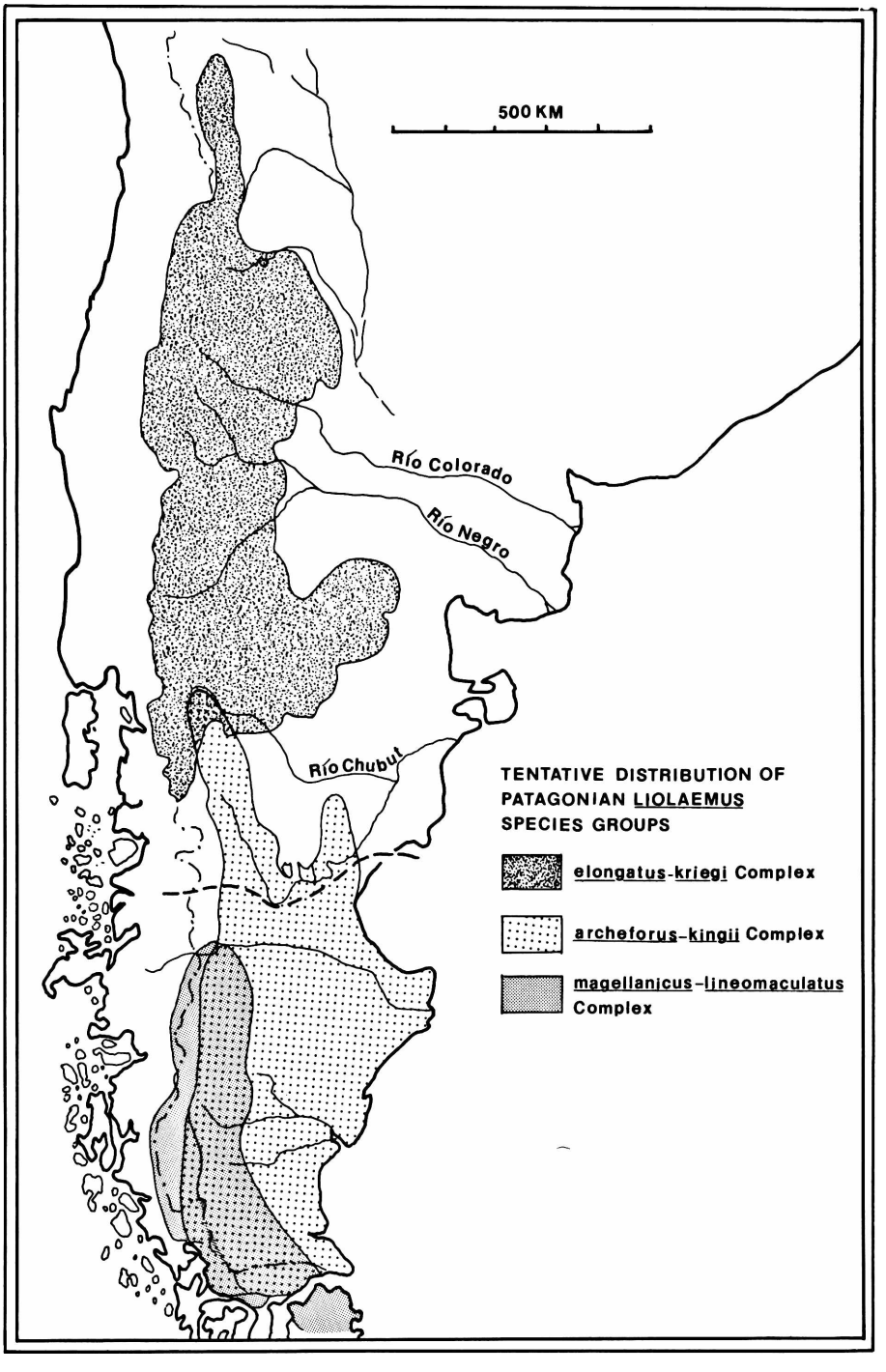

FIG. 13:17. Distributions of three *Liolaemus* species complexes in Patagonia.
Distribución de tres conjuntos específicos de Liolaemus *en Patagonia.*

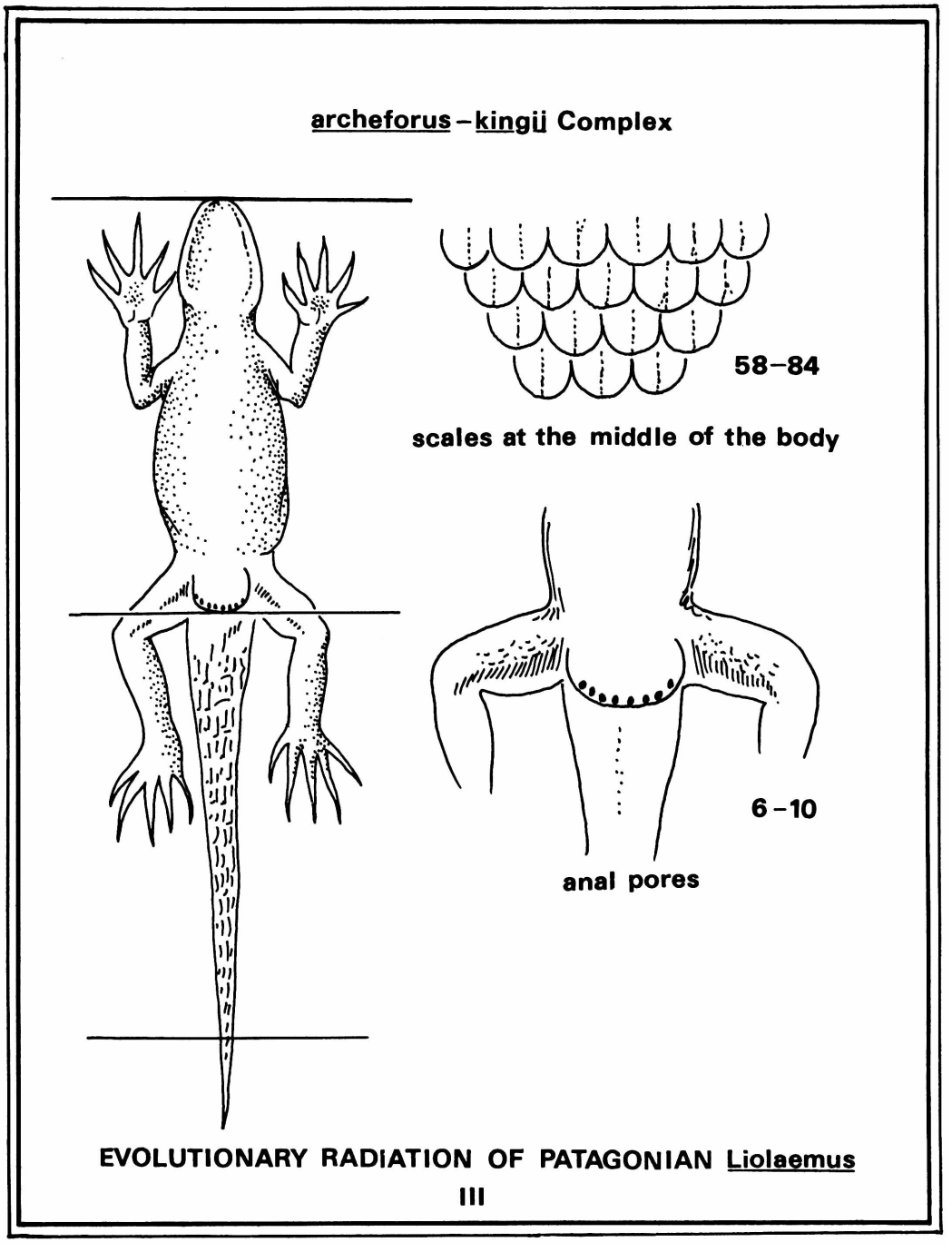

FIG. 13:18. Morphological traits of lizards of the *Liolaemus archeforus-kingii* complex.
Caracteristicas morfológicas de los saurios del conjunto Liolaemus archeforus-kingii.

elongatus or *austromendocinus* in Patagonian associations in southern Mendoza and with *L. elongatus* or *kriegi* in valleys in Neuquén. *Liolaemus buergeri* and *kriegi* occur in Patagonian habitats in Chile; presumably the transcordilleran migration was via Paso Pehuenche (2500 m, 36°S).

Several immunological cross-reactions among allopatric and sympatric populations of *L. austromendocinus* and *elongatus* show equally good specific levels of differentiation as among *L. elongatus, kriegi,* and *buergeri* (Cei, 1974a, 1975b).

Liolaemus kingii-archeforus *complex.*—This group is characterized by 1) no patch of enlarged scales on the posterior surface of the thigh (Fig. 13:18); 2) moderately high number (58–84) of faintly keeled scales around body; 3) high number (6–10) of preanal pores; 4) short legs and relatively short tail, only slightly longer than body; 5) venter with dark spots; absence of dark nuchal collar; 6) a series of yellowish or whitish transverse bars on the dark dorsal ground color.

Contents: *L. archeforus archeforus, L. archeforus sarmientoi, L. kingii.* This group is endemic to the southern faunal region (Fig. 13:17). *Liolaemus a. archeforus* occurs on the isolated Meseta de Lago del Sello; it is replaced by *L. a. sarmientoi* at lower elevations eastward in the Patagonian steppe between the Río Coyle and the Río Gallegos. *Liolaemus kingii,* which lies at a moderate serological distance from *L. archeforus,* is a rather stout, apparent ecological generalist inhabiting ravines and open bushy habitats in most of Santa Cruz. It reaches the Atlantic coast, and in the western part of its range is broadly sympatric with *L. archeforus.*

Liolaemus magellanicus–lineomaculatus *complex.*—This group is characterized by 1) no patch of enlarged scales on the posterior surface of thigh; 2) low number (40–70) of large, mucronate, acuminate (dorsally) scales around body; 3) moderate number (3–8) of preanal pores; 4) very short limbs and tail (Fig. 13:19); 5) absence of ventral melanism and dark nuchal collar; 6) dorsum irregularly spotted with black and having whitish longitudinal lines.

Content: *L. lineomaculatus, L. magellanicus.* The latter occurs in the humid southern lowlands on the mainland and in isolated populations on Tierra del Fuego, whereas *L. lineomaculatus* is found in the volcanic highlands in the ancient Patagonian region, where it inhabits open formations and *Araucaria* woodlands (Fig. 13:17). Occasional immaculate individuals of *L. lineomaculatus* are known (Cei, 1971a).

These last two complexes of *Liolaemus* are limited to austral Patagonia and are conservative in their diversity, as compared to the *Liolaemus fitzingeri* and *elongatus-kriegi* complexes, both of which apparently have undergone recent (post-Pleistocene) speciation. The results of these radiations are numerous morphologically similar species differing from one another biochemically and ecologically.

ACKNOWLEDGMENTS

In acknowledge the special interest and efforts of William E. Duellman in rewriting the original English draft of this manuscript and in his critical analysis of the distributional data. I also thank John D. Lynch for information about his research on the morphology and relationships of telmatobiine frogs in the Patagonian Region.

RESUMEN

Biologicamente, la Patagonia se define como la región al este de los Andes, extendiendose hasta el Oceano Atlántico, hacia el sur hasta el Estrecho de Magallanes; en el norte hay una zona de transición entre la biota patagónica y las del norte, entre los ríos Negro y Colorado.

La Patagonia es una región de suelos de rocas sedimentarias y mesetas de rocas efusivas, presentando severas sequías estacionales con cinco meses de invierno frío, veranos usualmente secos y clima fresco.

En contraste con las asociaciones de estepa uniformes que existen allí actualmente, una vegetación tropical y subtropical occurió al mismo tiempo que bosques xerofíticos y bos-

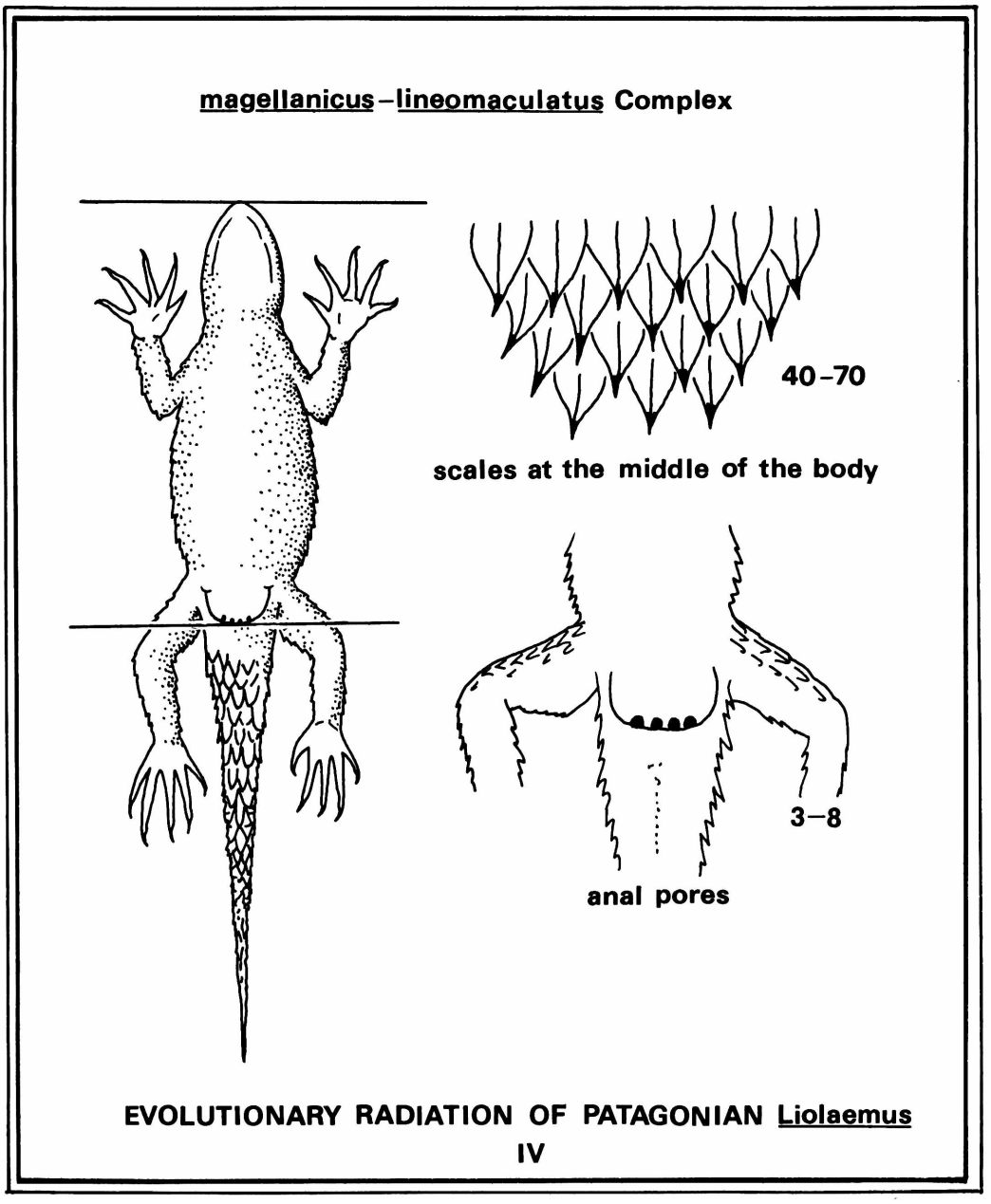

FIG. 13:19. Morphological traits of lizards of the *Liolaemus magellanicus–lineomaculatus* complex.

Caracteristicas morfológicas de los saurios del conjunto Liolaemus magellanicus–lineomaculatus.

ques mesofíticos de galeria durante el Oligoceno y el Mioceno. Bosques de *Nothofagus* existian durante el Eoceno y el Oligoceno. A mediados del Terciario los climas se volvieron más secos dando lugar a la expansión de la vegetación xerofítica.

En los depósitos del Oligoceno y del Mioceno telmatóbidos primitivos, ceratofrínidos, y bufónidos son conocidos, asi como boideos primitivos, cocodrilos, y tortugas meiolanidas y pelomedusidas están representados en los depósitos del Cretáceo superior y del Ceno-

zoico inferior. Los fósiles existentes, la presente distribución y los patrones de especiación indican que la Patagonia ha sido una región importante para la evolución de la herpetofauna austral.

Dos regiones faunísticas se reconocen en la Patagonia—1) la región del norte, o Patagonia antigua, 2) la región del sur, o de Santa Cruz. El límite entre estas dos regiones se encuentra aproximadamente en el Río Chubut, 45°S (Fig. 13:3).

La herpetofauna patagónica está compuesta de 60 especies: 14 anuros, 1 tortuga, 34 saurios, 11 ofidios. Hay un grado notable de endemismo. De las 60 especies, 56 ocurren el la región del norte, 13 especies en la región del sur, y nueve especies están representadas en ambas regiones. En la región del norte se encuentra la única tortuga y el único amphisbénido y todas las especies de ofidios y anuros, excepto una especie de rana (*Pleurodema bufonina*) y una especie de serpiente (*Bothrops ammodytoides*) que entran en la región del sur.

El grado de endemismo es alto, especialmente en los altiplanos volcanicos, en las estribaciones de los Andes y en las mesetas aisladas. Los géneros monotípicos *Somuncuria* y *Vilcunia* son endémicos de las mesetas asi como las especies y/o subespecies de *Alsodes*, *Atelognathus*, *Liolaemus*, y *Phymaturus*.

En la Patagonia ha habido temprana expansión adaptativa de los telmatóbidos de la familia Leptodactylidae. La región también fue el centro de evolución de las diversas líneas de iguánidos, y actualmente es un centro de especiación de *Liolaemus*. Cuatro grupos de especies de *Liolaemus* tienen su centro de dispersión en la Patagonia. Estos han sufrido especiación post-pleistocenica y sucesiva dispersión en la región, con el resultado de muchas líneas de especies afines bioquímica y ecológicamente bien definidas.

LITERATURE CITED

Barrio, A. 1973. Una nueva especie de *Telmatobius* (Anura, Leptodactylidae) procedente del dominio austral cordillerano Argentino. Physis 32C:207–213.

Berry, E. W. 1938. Tertiary flora from the Rio Pichi Leufu, Argentina. Geol. Soc. Amer. Spec. Pap. (12):1–149.

Bogart, J. P. 1970. Systematic problems in the amphibians family Leptodactylidae (Anura) as indicated by karyotypic analysis. Cytogenetics 9: 369–383.

Cabrera, A. L. 1951. Territorios fitogeográficos de la República Argentina. Bol. Soc. Argentina Bot. 4:21–65.

Casamiquela, R. M. 1963. Sobre un par de anuros del Mioceno de Rio Negro (Patagonia). *Wawelia gerholdi* n. gen. et sp. (Ceratophrydidae) y *Gigantobatrachus parodi* (Leptodactylidae). Ameghiniana 3:141–160.

Cei, J. M. 1969a. La meseta basáltica de Somuncurá, Río Negro. Herpetofauna endémica y sus peculiares equilibrios biocenóticos. Physis 28: 257–271.

Cei, J. M. 1969b. The Patagonian telmatobiid fauna of the volcanic Somuncura Plateau. J. Herpetol. 3:1–18.

Cei, J. M. 1970a. Fluctuaciones biocenóticas y relictos herpetológicos de la planicie de Lonco-Luán (Neuquén). Acta Zool. Lilloana 27:193–200.

Cei, J. M. 1970b. *Telmatobius solitarius* n. sp., a new rare telmatobiid frog from the highland Patagonian territories (Rio Negro, Argentina). Herpetologica 26:18–23.

Cei, J. M. 1971a. Herpetología Patagónica—I. *Liolaemus* del grupo *magellanicus*. Caracteristicas taxonómicas y genéticas. Physis 30:417–424.

Cei, J. M. 1971b. Herpetología Patagónica—II. Notas sobre la distribución geográfica del género *Diplolaemus*. Ibid. 30:471–474.

Cei, J. M. 1972a. Herpetología Patagónica—III. Relaciones de afinidad seroproteínicas y filéticas en el género *Liolaemus*. Ibid. 31:411–422.

Cei, J. M. 1972b. Herpetología Patagónica—V. Las especies extracordilleranas alto-Patagónicas del género *Telmatobius*. Ibid. 31:431–449.

Cei, J. M. 1973a. Herpetología Patagónica—VI. Los *Liolaemus* del grupo *fitzingeri* en Santa Cruz y Chubut (Sauria, Iguanidae). Ibid. 32C:447–458.

Cei, J. M. 1973b. Herpetología Patagónica—VII. Notas ecológicas y morfológicas sobre *Liolaemus bibroni* y *L. boulengeri*. Ibid. 32C:459–469.

Cei, J. M. 1973c. Comentarios sobre algunos géneros de iguánidos: *Diplolaemus*, *Leiosaurus*, *Aperopristis* y *Cupriguanus*. Ibid. 32C:269–276.

Cei, J. M. 1973d. Distribución geográfica y caracteres poblacionales de *Cupriguanus fasciatus* (D'Orbigny) (Sauria, Iguanidae). Ibid. 32C: 255–262.

Cei, J. M. 1974a. Revision of the Patagonian lizards of the *Liolaemus elongatus* complex. J. Herpetol. 8:219–229.

Cei, J. M. 1974b. Herpetología Patagónica—VIII. La altiplanicie entre Primeros Pinos y Río Kilka, Neuquén. Physis 33C:183–185.

Cei, J. M. 1975a. Herpetología Patagónica—IX. *Liolaemus goetschi* y el conjunto *Liolaemus darwini-boulengeri*. Ibid. 34C:199–202.

CEI, J. M. 1975b. Herpetología Patagónica—X. El conjunto evolutivo de *Liolaemus elongatus*: analisis serológico. Ibid. 34C:203–208.

CEI, J. M. 1975c. Herpetología Patagónica—XI. Diferenciación serológica de *Diplolaemus darwini* y *Diplolaemus bibroni* en poblaciones alosimpátridas. Ibid. 34C:209–210.

CEI, J. M. 1975d. *Lialaemus melanops* Burmeister and the subspecific status of the *Liolaemus fitzingeri* group (Sauria-Iguanidae). J. Herpetol. 9: 217–222.

CEI, J. M. 1975e. Southern Patagonian lizards of the *Liolaemus kingi* group. Herpetologica 31: 109–116.

CEI, J. M. 1976. Remarks on some Neotropical amphibians of the genus *Alsodes* from southern Argentina (Anura, Leptodactylidae). Atti Soc. Italia Sci. Nat. Mus. Civ. Stor. Nat. Milano 117: 79–84.

CEI, J. M. 1977. Serological relationships of the Patagonian toad *Bufo variegatus* (Günther). Serol. Mus. Bull. 52:2.

CEI, J. M. 1979. Amphibians of Argentina. Monit. Zool. Italiano Monog. Zool. (in press).

CEI, J. M., CASTRO, L. P. 1973. Taxonomic and serologic researches on the *Phymaturus patagonicus* complex. J. Herpetol. 7:237–247.

CEI, J. M., CASTRO, L. P. 1975. A serological contribution to the taxonomic status of *Cupriguanus*, a South American genus of iguanid lizards. Serol. Mus. Bull. 51:5–6.

CEI, J. M., ROIG, V. G. 1966. Caracteres biocenóticos de las lagunas basálticas del oeste de Neuquén. Bol. Est. Geog. Univ. Nac. Cuyo 13:182–201.

CEI, J. M., ROIG, V. G. 1968. Telmatobiinos de las lagunas basálticas de Neuquén (Anura, Leptodactylidae). Physis 27:265–284.

CEI, J. M., ROIG, V. G. 1975. A new lizard from the Sierra del Nevado Mountains, central Argentina. J. Herpetol. 9:256.

CEI, J. M., SCOLARO, J. A. 1977. Herpetología Patagónica—XIII. La identidad de *Liolaemus goetschi* y de la forma *melanops* del grupo *Liolaemus fitzingeri*, en Río Negro y Chubut. Physis 36C: 225–226.

CHAFFEE, R. G. 1952. The Deseadan vertebrate fauna of Scarritt Pocket, Patagonia. Bull. Amer. Mus. Nat. Hist. 98:509–562.

DONOSO-BARROS, R. 1966. Reptiles de Chile. Ed. Univ. Chile, Santiago, 458 p.

DONOSO-BARROS, R., CEI, J. M. 1971. New lizards from Patagonian volcanic tablelands of Argentina. J. Herpetol. 5:89–95.

DUELLMAN, W. E. 1966. The Central American herpetofauna: An ecological perspective. Copeia 1966(4):700–719.

DUELLMAN, W. E., VELOSO M., A. 1977. Phylogeny of *Pleurodema* (Anura: Leptodactylidae): A biogeographic model. Univ. Kansas Mus. Nat. Hist. Occas. Pap. (64):1–46.

ESTES, R., REIG, O. A. 1973. The early fossil record of frogs: A review of the evidence, pp. 11–63 *in* VIAL, J. L. (ed.). Evolutionary biology of the anurans: Contemporary research on major problems. Univ. Missouri Press, Columbia, 470 p.

GALLARDO, J. M. 1962. A propósito de *Bufo variegatus* (Günther) sapo del bosque húmedo Antartandico, y las otras especies de *Bufo* neotropicales. Physis 23:93–102.

GALLARDO, J. M. 1964. Los géneros *Urostrophus* D. & B. y *Cupriguanus* gen. n. (Sauria, Iguanidae) y sus especies. Neotropica 10:125–136.

GALLARDO, J. M. 1968. Dos nuevas especies de Iguanidae (Sauria) de la Argentina. Ibid. 14:1–8.

GALLARDO, J. M. 1970. A propósito de los Telmatobiinae (Anura, Leptodactylidae) patagónicos. Ibid. 16:73–85.

GASPARINI, Z. B., BÁEZ, A. M. 1975. Aportes al conocimiento de la herpetofauna terciaria de la Argentina. Acta I Congr. Argentino Paleontol. Biostrat. 2:377–413.

HARRINGTON, H. J. 1962. Paleogeographic development of South America. Bull. Amer. Assoc. Petrol. Geol. 46:1773–1814.

LYNCH, J. D. 1971. Evolutionary relationships, osteology, and zoogeography of leptodactyloid frogs. Univ. Kansas Mus. Nat. Hist. Misc. Publ. (53): 1–238.

LYNCH, J. D. 1978. A re-assessment of the telmatobiine leptodactylid frogs of Patagonia. Univ. Kansas Mus. Nat. Hist. Occas. Pap. (72):1–57.

MORELLO, J. 1958. La provincia fitogeográfica del monte. Opera Lilloana 2:5–115.

PETERS, J. A., DONOSO-BARROS, R. 1970. Catalogue of the Neotropical Squamata II. Lizards and amphisbaenians. Bull. U.S. Natl. Mus. (297):1–293.

RUIZ LEAL, A. 1972. Los confines boreal y austral de las provincias patagónicas y central respectivamente. Bol. Soc. Argentina Bot. 13 (Supplement):89–118.

SCHAEFFER, R. 1949. Anurans from the early Tertiary of Patagonia. Bull. Amer. Mus. Nat. Hist. 93:47–68.

SCOLARO, J. A., CEI, J. M. 1977. Herpetología Patagónica—XII. Los iguánidos del grupo *Liolaemus fitzingeri* en Chubut: datos serológicos y posición taxonómica. Physis 36C:219–223.

TIHEN, J. A. 1962. A review of the New World fossil bufonids. Amer. Midl. Nat. 68:1–50.

VUILLEUMIER, F. 1968. Origin of frogs of Patagonian forest. Nature 219:87–90.

APPENDIX

APPENDIX 13:1.—Distribution of species and subspecies of amphibians and reptiles in ten districts of the two major faunal regions in Patagonia.

Taxon	Northern Region					Southern Region				
	Monte	Monte-Patagonian Ecotone	Patagonian Steppe	Volcanic Highlands	Meseta de Somuncurá	Altiplano Central	Coastal District	Humid Southern Lowlands	Sub-Andean Area	Meseta del Lago de Sello
Anurans										
Alsodes gargola gargola	−	−	−	+	−	−	−	−	−	−
Alsodes gargola neuquensis	−	−	−	+	−	−	−	−	−	−
Atelognathus nitoi	−	−	−	+	−	−	−	−	−	−
Atelognathus patagonicus	−	−	−	+	−	−	−	−	−	−
Atelognathus praebasalticus praebasalticus	−	−	−	+	−	−	−	−	−	−
Atelognathus praebasalticus agilis	−	−	−	+	−	−	−	−	−	−
Atelognathus praebasalticus dobeslawi	−	−	−	+	−	−	−	−	−	−
Atelognathus praebasalticus luisi	−	−	−	+	−	−	−	−	−	−
Atelognathus reverberii	−	−	−	−	+	−	−	−	−	−
Atelognathus solitarius	−	−	+	−	−	−	−	−	−	−
Leptodactylus ocellatus	−	+	−	−	−	−	−	−	−	−
Odontophrynus occidentalis	+	+	−	−	−	−	−	−	−	−
Pleurodema bufonina	−	+	+	+	+	+	−	+	+	−
Pleurodema nebulosa	+	+	−	−	−	−	−	−	−	−
Pleurodema thaul	−	−	−	+	−	−	−	−	−	−
Somuncuria somuncuriensis	−	−	−	−	+	−	−	−	−	−
Bufo arenarum	+	+	−	−	−	−	−	−	−	−
Bufo spinulosus	−	−	+	+	−	−	−	−	−	−
Lizards										
Homonota darwinii	−	+	+	+	+	+	+	+	+	−
Homonota horrida	+	+	−	−	−	−	−	−	−	−
Ctenoblepharis donosobarrosi	+	+	−	−	−	−	−	−	−	−
Diplolaemus bibronii	−	−	+	−	−	+	+	+	+	−
Diplolaemus darwinii	−	−	+	+	+	+	+	−	−	−
Diplolaemus leopardinus	−	−	−	+	−	−	−	−	−	−
Leiosaurus bellii	−	+	+	−	−	−	−	−	−	−
Liolaemus archeforus archeforus	−	−	−	−	−	−	−	−	−	+
Liolaemus archeforus sarmientoi	−	−	−	−	−	−	−	+	−	−
Liolaemus austromendocinus	−	+	−	−	−	−	−	−	−	−
Liolaemus bibronii	−	+	+	+	+	+	+	−	−	−
Liolaemus boulengeri	−	+	+	+	+	+	+	−	−	−
Liolaemus buergeri	−	−	−	+	−	−	−	−	−	−
Liolaemus ceii	−	−	+	+	−	−	−	−	−	−
Liolaemus chilensis	−	−	−	+	−	−	−	−	−	−
Liolaemus darwinii	+	+	−	−	−	−	−	−	−	−
Liolaemus elongatus elongatus	−	−	+	+	−	−	−	−	−	−
Liolaemus elongatus petrophilus	−	−	−	−	+	−	−	−	−	−
Liolaemus fitzingeri fitzingeri	−	−	−	−	−	+	+	−	+	−
Liolaemus fitzingeri canqueli	−	−	+	−	−	−	−	−	−	−
Liolaemus fitzingeri melanops	+	+	−	−	−	−	−	−	−	−
Liolaemus gracilis	+	+	−	−	−	−	−	−	−	−
Liolaemus kingii	−	−	−	−	−	+	+	−	+	−
Liolaemus kriegi	−	−	+	+	−	−	−	−	−	−
Liolaemus lineomaculatus	−	−	−	+	−	−	−	+	−	+
Liolaemus magellanicus	−	−	−	−	−	−	−	+	−	−
Liolaemus rothi	−	−	+	+	+	−	−	−	−	−

APPENDIX 13:1 (Concluded).

Taxon	Northern Region					Southern Region				
	Monte	Monte-Patagonian Ecotone	Patagonian Steppe	Volcanic Highlands	Meseta de Somuncurá	Altiplano Central	Coastal District	Humid Southern Lowlands	Sub-Andean Area	Meseta del Lago de Sello
Liolaemus ruizleali	−	−	−	−	+	−	−	−	−	−
Liolaemus tenuis	−	−	−	+	−	−	−	−	−	−
Phymaturus palluma	−	−	−	+	−	−	−	−	−	−
Phymaturus patagonicus patagonicus	−	−	+	−	−	−	−	−	−	−
Phymaturus patagonicus indistinctus	−	−	+	−	−	−	−	−	−	−
Phymaturus patagonicus somuncurensis	−	−	−	−	+	−	−	−	−	−
Phymaturus patagonicus zapalensis	−	−	−	+	−	−	−	−	−	−
Pristidactylus fasciatus	+	+	+	+	−	−	−	−	−	−
Proctotretus pectinatus	−	+	−	−	−	−	−	−	−	−
Vilcunia sylvanae	−	−	−	−	−	−	−	−	−	+
Mabuya frenata	−	+	−	−	−	−	−	−	−	−
Cnemidophorus longicauda	+	+	−	−	−	−	−	−	−	−
Amphisbaenians										
Amphisbaena angustifrons	−	+	−	−	−	−	−	−	−	−
Snakes										
Leptotyphlops australis	+	+	−	−	−	−	−	−	−	−
Leptotyphlops borrichiana	+	+	−	−	−	−	−	−	−	−
Elapomorphus bilineatus	−	+	−	−	−	−	−	−	−	−
Leimadophis sagittifer	+	+	−	+	−	−	−	−	−	−
Lystrophis semicinctus	−	+	−	−	−	−	−	−	−	−
Philodryas burmeisteri	+	+	−	−	−	−	−	−	−	−
Philodryas patagoniensis	−	+	−	−	−	−	−	−	−	−
Philodryas psammophideus	+	+	−	−	−	−	−	−	−	−
Pseudotomodon trigonatus	+	+	−	−	−	−	−	−	−	−
Micrurus frontalis	−	+	−	−	−	−	−	−	−	−
Bothrops ammodytoides	+	+	+	+	−	+	+	−	−	−
Turtles										
Geochelone donosobarrosi	−	+	−	−	−	−	−	−	−	−
Total Taxa	17	32	18	29	11	9	8	6	4	3
Total Species	17	32	17	25	11	9	8	6	4	3