

A QUANTITATIVE SURVEY OF SPECIATION PHENOMENA IN PATAGONIAN BIRDS

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Resumen. Se define Patagonia como América del Sur desde 36°S hasta 56°S, una región de aproximadamente 1.140.000 kilómetros cuadrados, con una superficie equivalente a la Península Escandinávica en el hemisferio norte o a Colombia en la zona tropical, pero 4,4 veces mas grande que Nueva Zelandia en el hemisferio sur y en latitudes semejantes. Durante el Terciario los cambios de clima y vegetación fueron notables. Durante el Cuaternario un glaciar enorme cubrió una parte extensa de Patagonia y retrocedió según un ciclo que se repitió varias veces. Tomando en cuenta esta historia turbulenta, estudios de algunos géneros de aves patagónicas han correlacionado esquemas de especiación con eventos del Cuaternario. Se estudiaron las 217 especies de aves terrestres y acuáticas de Patagonia pero no las 11 especies oceánicas para cuantificar patrones de especiación en la avifauna entera. Setenta y tres especies (34%) presentan evidencia de cuatro fenómenos especiacionales. (1) Se estableció vicarianza local (alo- o parapatria de especies hermanas dentro de Patagonia) en 24 especies (11%). (2) Se descubrió vicarianza extra-Patagónica (alopatria de especies hermanas, con una o más especies fuera de Patagonia) en 31 especies (14%). (3) Se identificaron superposiciones de distribución debidas a simpatria secundaria en 25 especies (12%). Además, unas 15 especies (7%) representan relictos. Se supone que muchos patrones de especiación son de origen Pleistocénico, pero hay otros mucho mas antiguos. Futuras investigaciones permitirán más fina reconstrucción de la historia especiacional de las aves patagónicas. Tales reconstrucciones deberán incluir los extensos datos geológicos y paleoecológicos ya disponibles para el extremo sur del continente Sudamericano.

Abstract. Patagonia is southernmost South America between 36°S and 56°S, an area of about 1,140,000 square kilometers, equivalent to Fennoscandia in the northern hemisphere or Colombia in the tropics but 4.4 times larger than New Zealand at similar latitudes in the southern hemisphere. During the Tertiary major changes in climate and vegetation occurred. During the Quaternary a huge icecap covered much of Patagonia and then retreated, a cycle that was repeated several times. Against this turbulent background, studies of selected genera of Patagonian birds have ascribed speciation patterns to Quaternary events. To quantify speciation in the entire fauna, all 217 species of breeding land and waterbirds were surveyed (the 11 oceanic taxa were excluded), and the presence/absence of four patterns were tabulated. Seventy-three species (34%) exhibit speciation patterns. Local vicariance (allo- or parapatry of sister species within Patagonia) was detected in 24 species (11%). Extra-Patagonian vicariance (allopatry of sister taxa, with one or more outside Patagonia) was found in 31 species (14%). Overlaps due to secondary sympatry were identified in 25 species (12%). About 15 species (7%) are relict taxa representing former speciation. Whereas many speciation patterns are probably of Pleistocene origin, others are clearly much older. Only further research will permit ornithologists to trace better the speciation history of birds in Patagonia, and to correlate it with the detailed geological and paleoecological reconstructions available in the literature. *Accepted 7 January 1991.*

Keywords: *Speciation, vicariance, Patagonia, South America, avifauna, Pleistocene events, biogeography.*

INTRODUCTION

Patagonia (south-temperate South America) has had a complex geological and vegetational history in the Tertiary (Harrington 1962, Menéndez 1971, Romero 1986) and the Quaternary (Pleistocene-Holocene; Auer 1958, 1970; Heusser 1989, Markgraf 1983, 1989; Mercer 1976, Mercer *et al.* 1975). In the Late Pleistocene western Patagonia was covered by the largest icecap in South America (480,000 km², Hollin & Schilling 1981). A substantial area of Patagonia

was therefore uninhabitable during this and earlier glacial advances. The fauna must either have "retreated" elsewhere, or have suffered extinctions (Markgraf 1985). By greatly affecting the distribution of vegetation types and markedly altering the width of continental margins, glacial-interglacial cycles must have had major impacts on the avifauna.

To reconstruct the effects of historical events on selected taxa, detailed studies have been made by Humphrey and his co-workers on nonpas-

serine littoral genera (especially *Phalacrocorax* and *Tachyeres*) and by Vuilleumier and his co-workers on passerine landbird genera (especially *Geositta* and *Phrygilus*). This ongoing research has demonstrated that past environmental factors, probably Pleistocene in age, have indeed promoted the formation of new species of both waterbirds and landbirds in Patagonia. Because the Pleistocene-Holocene history of climate and vegetation in Patagonia is already known in considerable detail (Markgraf 1989) this region offers great promise for avian evolutionists interested in speciation.

To evaluate historical impacts on the entire Patagonian avifauna in quantitative terms — and

to provide a background analysis useful for further research — I surveyed speciation patterns in all 137 genera and 217 species of breeding land and waterbirds, thus extending an earlier analysis restricted to 46 landbird species living in *Nothofagus* forests (Vuilleumier 1985) and a qualitative review of all Patagonian birds (Vuilleumier 1990, 1991). In this paper I seek preliminary answers to three questions. (1) How many extant Patagonian species show evidence of (allopatric) speciation? (2) How widespread geographically and ecologically were vicariance events in Patagonia? (3) How many extant species originated due to Pleistocene versus older factors? A fourth question, whether speciation is more active in Pata-

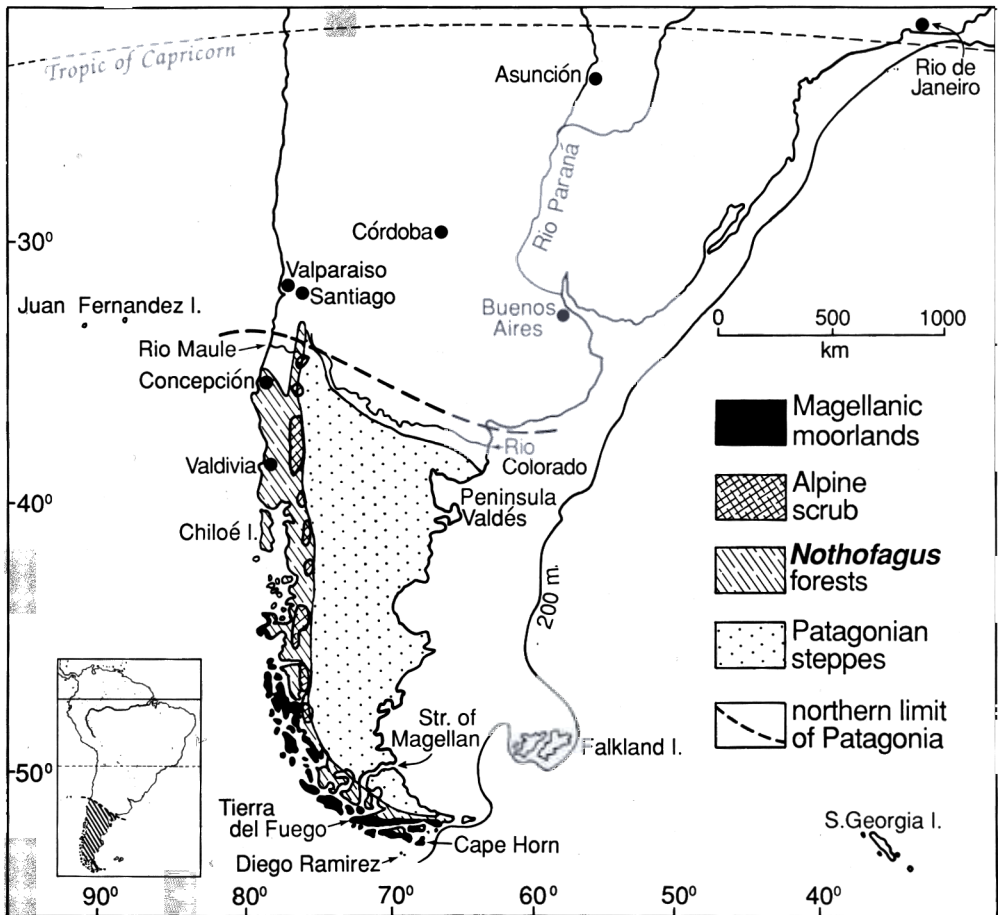


FIG. 1. Schematic map of temperate South America showing the location of Patagonia and its four main vegetation types: Magellanic moorlands, *Nothofagus* forests, alpine scrub, and steppes.



FIG. 2. The Patagonian icecap viewed from a commercial aircraft at about 8,000 m and at about 50°S, showing glacial tongues calving into Patagonian lakes east of the Andes. Photo F. Vuilleumier, February 1987.

gonia than in other, comparable regions, in South America or elsewhere, is not dealt with here.

DEFINITIONS, DATA BASE, ASSUMPTIONS, AND METHODS

Patagonia

Patagonia in southern South America is defined ecologically by the presence of *Nothofagus* forests in the west and arid steppes in the east. It encompasses about 1,140,000 square kilometers from the Rio Maule (Chile, 36°S) westward to the Rio Colorado (Argentina, 38°S) and southward to Cape Horn (56°S) (Fig. 1). In the SW Pacific, Patagonia would fit between Canberra (36°S), Geelong (38°S), and Macquarie Island (55°S). Its area is 4.4 times larger than that of New Zealand. Fennoscandia or Tibet in Eurasia, and Colombia in South America, have areas similar to Patagonia's. The Patagonian littoral is extensive and rugged, with a variety of avian habitats (Murphy 1936). Rivers are few and short, but lakes are numerous and some are very large (Lago Buenos

Aires is among the largest water bodies in South America). Salt flats and brackish lagoons are locally numerous and extensive. No other region of comparable area in South America shows the influence of Pleistocene glacial geology as dramatically as does Patagonia. The present icecap (Fig. 2) covers about 19,500 km² (Hollin & Schilling 1981) and is the largest icecap in South America. Climatically, Patagonia is cool and windy (Endlicher & Santana 1988).

Vegetation types

The four major vegetation formations of Patagonia (Fig. 1) are Magellanic moorlands along the Pacific margin (Moore 1979, Pisano 1983), *Nothofagus* (beech) rainforests along the Andes (Young 1972, McQueen 1976), alpine moorlands above timberline (Moore 1975), and steppes and semi-deserts from the eastern Andean foothills to the Atlantic Ocean (Soriano 1983). The two dominant vegetation types are forests and steppes (Cabrera 1971, Hueck & Seibert 1972, Pisano 1981). Steppes are more extensive than forests and located on plateaus (mesetas), and



FIG. 3. Lowland *Nothofagus* forest at about 52°S near Rio Rubens, NW of Punta Arenas, Magallanes, Chile. Note abundance of dead branches on the ground. Photo F. Vuilleumier, February 1987.

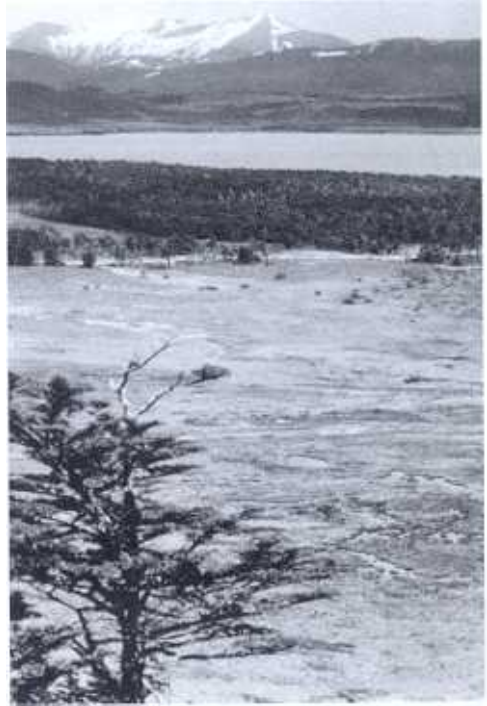


FIG. 4. Interdigitation of lowland *Nothofagus* forest and bog vegetation (foreground), and of forest and alpine scrub (background) at about 53°S, Peninsula Brunswick, S of Punta Arenas, Magallanes, Chile. Photo F. Vuilleumier, November 1985.

range from grassy to scrubby to semi-desert along a decreasing west-east moisture gradient. Figs. 3–6 illustrate the main vegetation types.

Avifauna

The Patagonian avifauna includes 228 breeding species (11 oceanic, 52 aquatic, and 165 terrestrial). The *Nothofagus* forest fauna has been described earlier in detail (Vuilleumier 1985). A comparable analysis for the steppe fauna is now in preparation. For this survey I excluded the 11 oceanic species (Spheniscidae, Diomedidae, Procellariidae, Hydrobatidae, Pelecanoididae, Sulidae), and analyzed 217 species (52 aquatic, 165 terrestrial) in 137 genera. The Patagonian avifauna is depauperate. Equatorial Colombia (same area) has 1500 species (Hilty & Brown 1986). Subtropical-temperate Tibet (same area) has 400 species (Vaurie 1972). But other ecologically

extreme regions also have few species. Thus, land-locked and desert Mongolia (larger) has 285 species (Vaurie 1964), and cool-temperate-arctic Alaska (larger), at the northwestern tip of the Western Hemisphere, has 235 species (Armstrong 1990).

Distributional data

Information on distribution was extracted from Araya *et al.* (1986), Clark (1986), Hellmayr (1932), Humphrey *et al.* (1970), Olrog (1979), Peters (1923), Philippi (1964), and Venegas (1986). Several periods of field work (February–March 1965, November–December 1985, February–March 1987, October 1987, January 1988, November 1988) permitted me to collect specimens and distributional data and to interpret distribution of species and communities in ecological terms.



FIG 5. Top: alpine moorland at about 650 m on Navarino Island, about 55°S, Magallanes, Chile. Photo F. Vuilleumier, November 1985. Bottom: boggy mountaintop vegetation with cushion plants and heath at about 550 m, Sierra Boquerón, near Porvenir, about 53°S, Tierra del Fuego, Magallanes, Chile. Photo F. Vuilleumier, February 1987.



FIG. 6. Top: dry, open grassy steppe, mainland near Pali-Aike (S of Rio Gallegos), about 52°S, Magallanes, Chile. Photo F. Vuilleumier, February 1987. Bottom: moist, dense grassy steppe with *Chilictrichum* scrub (and guanacos), about 53°S, near Bahia Felipe, Tierra del Fuego, Magallanes, Chile. Photo F. Vuilleumier, November 1985.

Taxonomic data

Information on the taxonomy of Patagonian birds was extracted from the literature (many references in Vuilleumier 1985). Study of museum specimens (especially at the American Museum of Natural History, New York; the Museum of Comparative Zoology, Cambridge, Massachusetts; the National Museum of Natural History, Washington, D.C.; the Peabody Museum, Yale University; the Instituto de la Patagonia, Punta Arenas; and the Instituto Miguel Lillo, Tucumán) allowed me to evaluate the taxonomic conclusions of others.

Assumptions

Three major assumptions are made in this review. (1) Speciation is allopatric and proceeds along the lines described by Mayr (1963). (2) Analysis of geographic isolation and differentiation, secondary contacts (including parapatry and hybridization), and secondary range overlaps between or among sister species, permit one to attempt the reconstruction of vicariance events. The concept of superspecies (Mayr 1963, Amadon 1966) is accepted and used when appropriate. (3) Geological and paleobotanical evidence can be used as a guide to interpreting avian distributional evidence (Vuilleumier 1980).

Methods

After compiling a list of species of breeding birds of Patagonia, I analyzed geographical and ecological distribution together with taxonomic and phylogenetic evidence about nearest relative(s) of each species. Since only a small number of species have been studied in detail to date, a survey of the entire Patagonian avifauna at this time is based on relatively crude evidence. Thus, for instance cladistic analyses must await another level of approach to be used for the whole fauna. Hopefully, other workers will thus be spurred to seek new evidence in order to demolish my conclusions.

SPECIATION

Devillers & Terschuren (1978) and Livezey (1986) have published detailed hypotheses to explain speciation patterns in *Phalacrocorax* and *Tachyeres*, respectively, invoking vicariance events associated with glaciation and deglaciation cycles in the last 100,000 years. In these sce-

narios the major barrier that isolated Pacific from Atlantic coast populations of ancestral taxa was the western Patagonian icecap. Melting of the ice barrier permitted secondary contact, and another glacial advance provided another cycle of vicariance or geographic isolation. Accepting these reconstructions as general models that follow allopatric speciation theory (Mayr 1963, Bush 1975), one may thus envision a sequence of spatio-temporal events of the sort described by Vuilleumier (1980). (1) An ancestral species becomes split into geographical isolates because of an extrinsic barrier (vicariance event). (2) Genetic divergence in the geographical isolates leads to incipient or complete speciation. (Note that steps 1 and 2 can take place within the region or that the barrier can occur between the region and another.) (3) Barrier breakdown permits the former isolates to expand their ranges and come in secondary contact (parapatry). (4) Depending on the extent of reproductive isolation either hybridization or range overlap may take place. (5) If such a cycle is repeated several times several episodes of isolation and secondary contact can result in complex overlap patterns among sister species. An alternative to 5 is that extinctions at some point along this sequence will eliminate all but one of the evolving new species; the surviving taxon thus appears as a relict without close taxonomic allies. Yet another possibility, phyletic evolution, discussed previously (Vuilleumier 1967a) will not be analyzed again here.

Applying this five-step sequence of spatio-temporal events I have tabulated the presence of four speciation patterns in Patagonian taxa (Table 1): (1) local vicariance (allo- or parapatric taxa at the species level within Patagonia; in other words, the barrier separated populations within Patagonia); (2) extra-Patagonian vicariance (the barrier separated Patagonian from non-Patagonian populations, now allospecies or species); (3) overlaps (pairs of species showing secondary sympatry patterns with an intra-Patagonian origin); and (4) relicts (endemic or near-endemic species with no clearcut relatives living today).

LOCAL VICARIANCE

Twelve of 137 genera (9%) and 24 of 217 species (11%) show evidence of current or former local vicariance followed by incipient to full spe-

TABLE 1. Genera of Patagonian birds showing speciation phenomena. The Patagonian avifauna has 137 genera (100%) and 217 species (100%) of water and landbirds. The symbol "+" means presence of a given phenomenon, and "-" its absence, in a given genus. "Local Vicariance" means currently allopatric or parapatric species-level taxa within Patagonia. "Extra-Patagonian Vicariance" means currently allopatric species-level taxa including at least one Patagonian and at least one other taxon distributed disjunctly elsewhere in South America, or in another part of the world. "Overlaps" means moderately to broadly sympatric, closely related species-level taxa (sister species) within Patagonia. "Relicts" means species- or genus-level taxa restricted (endemic), or largely restricted to Patagonia, and lacking close relatives in or outside Patagonia. "No. of Species Involved" are Patagonian species only. An asterisk (*) indicates hybridization between closely related species.

Genus	Vicariance Events		Overlaps Relicts	No. of Species Involved	References
	Local	Extra-Patagonian			
<i>Tinamotis</i>					Vuilleumier 1986
<i>Podiceps</i>			+	2	Fjeldså 1982
<i>Phalacrocorax</i>	+			1	Devillers & Terschuren 1978
<i>Chloephaga</i>				4	Johnsgard 1978
<i>Tachyeres</i>	+				Livezey 1986
<i>Anas</i>					Johnsgard 1978
<i>Buteo</i>					Vuilleumier 1985
<i>Phalcoeboenus</i>				2	Vuilleumier 1970
<i>Haematopus</i>			+	3	Jehl 1978
<i>Charadrius</i>				2	Bock 1958
<i>Pluvianellus</i>				1	Jehl 1975
<i>Attagis</i>			(?)	2	Vuilleumier unpubl. data
<i>Thinocorus</i>			+	2	Vuilleumier unpubl. data
<i>Gallinago</i>				1	Olrog 1962
<i>Catharacta</i>	+			2	Devillers 1978
<i>Larus</i>				1	Devillers 1977
<i>Columba</i>				1	Vuilleumier 1985
<i>Enicognathus</i>				2	Vuilleumier 1985
<i>Colaptes</i>				1	Short 1972
<i>Picoides</i>					Short 1975
<i>Campephilus</i>				1	Short 1970
<i>Geositta</i>				2	Vuilleumier unpubl. data
<i>Eremobius</i>				1	Vaurie 1980
<i>Cinclodes</i>				2	Vuilleumier unpubl. data
<i>Sylvioorthorhynchus</i>				1	Vuilleumier 1985
<i>Apibrastura</i>				1	Vuilleumier 1985
<i>Asthenes</i>				3	Vuilleumier unpubl. data
<i>Pygarrhichas</i>				1	Vuilleumier 1985
<i>Pteroptochos</i>				2	Vuilleumier 1985
<i>Scelorchilus</i>				1	Vuilleumier 1985
<i>Eugralla</i>				1	Vuilleumier 1985
<i>Scytalopus</i>				1	Vuilleumier 1985
<i>Agriornis</i>				2	Vuilleumier 1971
<i>Neoxolmis</i>				2	Vuilleumier 1971, Lanyon 1986
<i>Xolmis</i>					Vuilleumier 1985
<i>Muscisaxicola</i>				4	Vuilleumier 1971
<i>Colorhampus</i>					Vuilleumier 1985, Lanyon 1986
<i>Phytotoma</i>					Short 1975
<i>Tachycineta</i>					Short 1975
<i>Mimus</i>					Short 1975
<i>Anthus</i>					Hall 1961, Murphy 1923
<i>Curvaeus</i>					Vuilleumier 1985
<i>Sicalis</i>					Vuilleumier unpubl. data
<i>Phrygilus</i>	+			3	Vuilleumier unpubl. data
<i>Melanodera</i>				2	Rand 1955, Vuilleumier 1985
Number of taxa:	26		11	14	

ciation. Eight cases have been described (*Phalacrocorax*, Devillers & Terschuren 1978; *Tachyeres*, Livezey 1986; *Phalacroboenus*, Vuilleumier 1985; *Scytalopus*, Vuilleumier 1985; *Agriornis*, Vuilleumier 1971; *Phrygilus*, Vuilleumier 1985). The eco-geography of isolation in these taxa corresponds to several kinds of barriers, including a river (the Bío-Bío in Chile), the Andes, and coastal areas. In the three instances analyzed in greatest detail (*Phalacrocorax*, *Tachyeres*, *Catharacta*) vicariance has been ascribed to Pleistocene factors (glacial advances). In other cases (*Asthenes*, *Agriornis*) the large morphological differences between allopatric species suggest that vicariance took place before the Pleistocene. I discuss two examples below, one unpublished and the other under study.

(1) *Aphrastura spinicauda* (family Furnariidae) is a geographically variable species (Fig. 7) that occurs from NW Patagonia southward to Cape Horn in or at the edge of *Nothofagus*

forests (Vuilleumier 1985) (Fig. 8 top). This species is perhaps the quintessential *Nothofagus*-inhabiting passerine. In an earlier paper (Vuilleumier 1967b: 401), I described it as "an arboreal species occupying two foraging niches, being a foliage as well as a trunk gleaner." Further (p. 401), I also wrote that "With quick and nervous motions they either cling acrobatically to twigs in the manner of titmice (*Parus*), or climb tree trunks exactly like treecreepers (*Certhia*)." Near the southern end of its range, however, *A. spinicauda* also lives locally in more open habitats: degraded woodlands with a second-growth scrub understory in Tierra del Fuego (Vuilleumier, pers. obs.), and shrubs on some islands of the Cape Horn archipelago (Reynolds 1935; Olrog 1950). Unexpectedly, *A. spinicauda* is not only present but also the most abundant land bird on subantarctic Diego Ramirez, a group of small islands 100 km SW of Cape Horn in Drake Passage, identified on Fig. 1 (Pisano & Schlatter



FIG. 7. Geographical variation in *Aphrastura* (Furnariidae). Three top specimens are *A. spinicauda*: top from Neuquén, Argentina, about 40°S; second from False Cape Horn (Hoste Island), Chile, about 55°S; third from Ancud, Chiloé Island, about 42°S, Chile. Bottom specimen: *A. masafueriae* from Juan Fernandez Islands. Note differences in size and color of underparts. All specimens from American Museum of Natural History. Photo AMNH.



FIG. 8. Top: breeding habitat of *Aphrastura spinicauda* with nesting hole in *Nothofagus* tree trunk, Peninsula Brunswick, S of Punta Arenas, about 53°S, Magallanes, Chile. Bottom: *A. spinicauda* near ground in subantarctic *Poa flabellata* grassland, Diego Ramirez Islands, Chile. Photos F. Vuilleumier, November 1985.

1981 ab, Venegas 1982, Vuilleumier, pers. obs.). The Diego Ramirez population is morphologically differentiated (Vuilleumier, pers. obs.; Schlatter, pers. comm.) and evidently reached these islands by dispersal over the sea. What is remarkable about *A. spinicauda* on Diego Ramirez is that it lives in tussock grassland of *Poa flabellata* (Fig. 8 bottom), where it behaves like a wren (*Cistothorus palustris*), rather than a titmouse (*Parus*) or a treecreeper (*Certhia*), and where its neighbors are albatrosses (*Diomedea chrysostoma* and *D. melanophris*). There are no woody plants on Diego Ramirez, which has subantarctic vegetation, like that of South Georgia. I did not succeed in finding nests, unfortunately, but saw several birds with food in their bill, pre-

sumably carrying it to their nestlings. I assume the nests were either in cavities within the base of dense tussocks of *Poa* or in petrel (*Halobaena*, *Pelecanoides*) burrows under the vegetation.

This situation is a case of vicariance with habitat shift and slight differentiation at the periphery of the species' range. (Note that *Aphrastura*, a good colonist, has reached the Juan Fernandez Islands, about 650 km W of central Chile, an instance of extra-Patagonian vicariance with species-level differentiation; Vaurie 1980, Vuilleumier 1985, Brooke 1988; see location of Juan Fernandez Islands on Fig. 1, and illustration of specimen from Juan Fernandez on Fig. 7 bottom.)

(2) *Phrygilus patagonicus* (family Emberizidae) lives in and at the edge of *Nothofagus* forests whereas its allo- or parapatric sister taxon, *P. gayi*, lives in steppes (Vuilleumier 1985, 1986) (Fig. 9; Fig. 10). The distribution pattern of these two sister taxa is very complex at the forest-steppe interface, at least locally (Humphrey *et al.* 1970). Since 1985 I have studied this situation at a number of sites across the Strait of Magellan (Fig. 10), and have collected about 115 specimens. What is probably a hybrid swarm has been discovered in NW Tierra del Fuego near a relictual woodland of *Drimys winteri* (Fig. 11 top). The woodland itself is inhabited by a population of pure *P. patagonicus*, but hybrids have been collected nearby (Fig. 11 bottom). Another hybrid swarm might exist in a valley a few km east of Porvenir, where the birds are found in a vegetation consisting mostly of dense scrub (matorral) growing on moraines (Fig. 12). *Nothofagus* stands on the mainland (Fig. 9 left) and on the island of Tierra del Fuego (Fig. 13) house only pure *patagonicus* phenotype, whereas steppes nearby appear to have only pure *gayi* phenotype. But in NW Tierra del Fuego a mosaic of populations has been sampled, showing the gamut from one phenotype to the other. Speciation is thus incomplete. The identification of the vicariance event that originally separated the common ancestor to *patagonicus* and *gayi* is made difficult by the fact that one taxon occupies forests and the other steppes. Speciation in these birds has been accompanied by a major habitat shift. Since all taxa in the genus *Phrygilus* other than *patagonicus* live in steppe-like envi-



FIG. 9. Left: characteristic breeding habitat of *Phrygilus patagonicus* in *Nothofagus* forest, Peninsula Brunswick, S of Punta Arenas, about 53°S, Magallanes, Chile. Photo F. Vuilleumier, November 1985. Right: characteristic breeding habitat of *Phrygilus gayi* in *Lepidophyllum* scrub, Punta Dungeness, about 52°30'S, Magallanes, Chile. Photo F. Vuilleumier, February 1987.

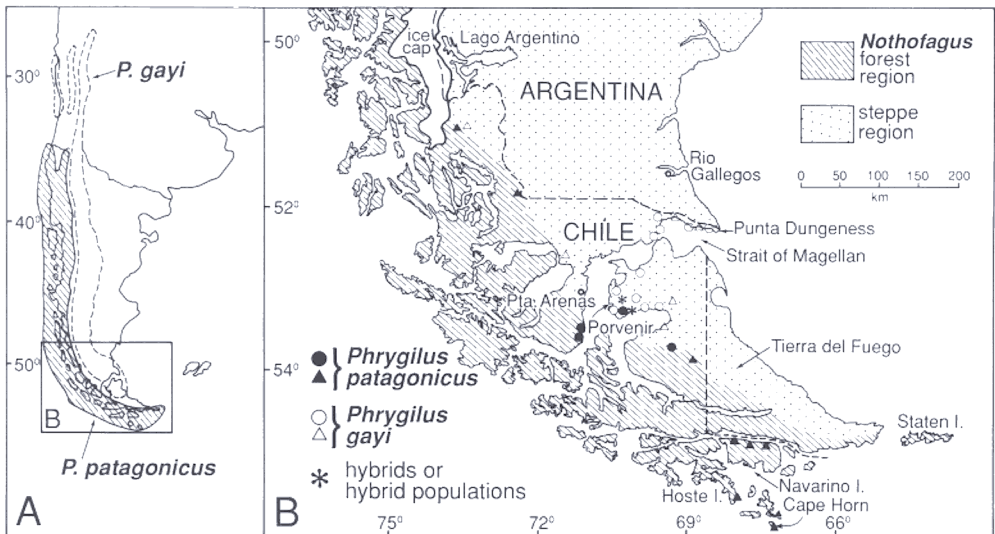


FIG. 10. A. Schematic map of the distribution of two allo- or parapatric sister species, forest-dwelling *Phrygilus patagonicus*, and steppe-inhabiting *P. gayi*. B. Distribution of *Phrygilus patagonicus* and *P. gayi* in southern Patagonia, based on unpublished field work. Both species are largely allopatric, but hybridization has been detected in two areas (indicated with *). Circles indicate specimens collected; triangles indicate observations. Note occurrence of *P. patagonicus* on Hoste Island and Cape Horn Island in southernmost *Nothofagus* patches.



FIG. 11. Top: relictual woodland of *Drimys winteri*, E of Porvenir, Tierra del Fuego, about 53°S, Magallanes, Chile. Woodland is habitat of *Phrygilus patagonicus* near hybrid population; coastal scrub in background is habitat of *P. gayi*. Photo F. Vuilleumier, October 1987. Bottom: evidence of hybridization between *Phrygilus patagonicus* and *P. gayi*; parents and their three nestlings collected at nest; left, *gayi* × *patagonicus* hybrid female, center, three nestlings, right, pure *patagonicus* male. Photo AMNH.

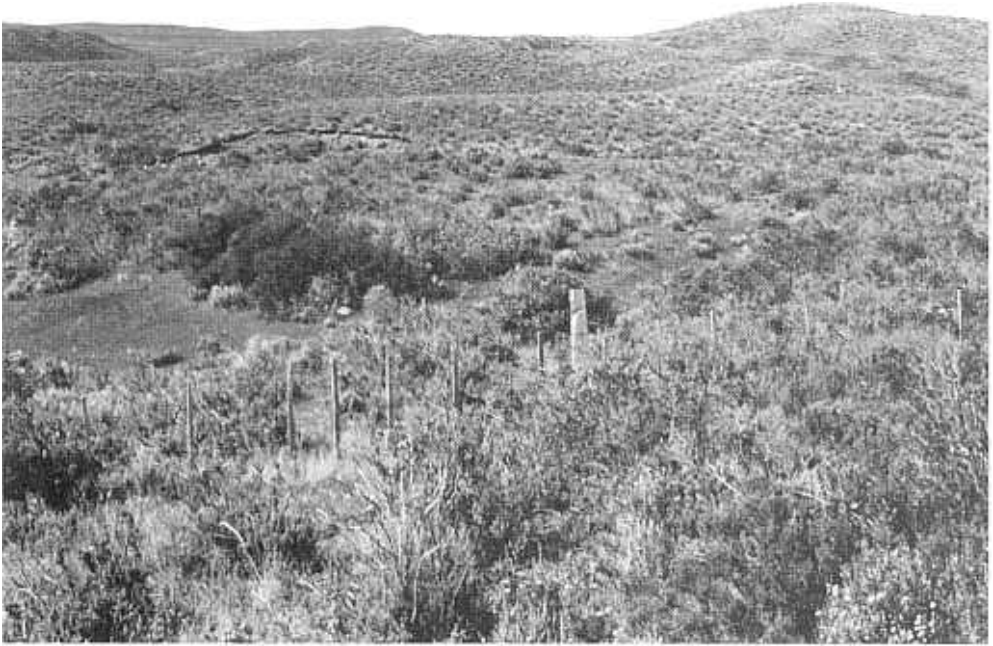


FIG. 12. Two views of dense scrub E of Porvenir at foot of Sierra Boquerón, Tierra del Fuego, about 53°S, Magallanes, Chile, where hybrids between *Phrygilus patagonicus* and *P. gayi* have been collected. Photo F. Vuilleumier, February 1987.

ronments (about 10 species in the Andes and Patagonia), the shift clearly took place from steppe to forest. A clue to the origin of the shift may be given by the observation that on Navarino Island, where *patagonicus* is abundant but where *gayi* does not occur, *patagonicus* occupies scrubby second-growth roadside habitats physiognomically and vegetationally similar to scrub on the mainland, where only *gayi* is found and is abundant. Thus, in the absence of one species the other increases the breadth of its habitat-niche. Fig. 14 illustrates the habitat shift within *P. patagonicus*. Morphological, biochemical, and paleobotanical data collected in the contact zone are being studied to shed more light on the evolution of these two taxa.



FIG. 13. *Nothofagus* forest, characteristic habitat of *Phrygilus patagonicus* on the island of Tierra del Fuego, Russfin, SE of Porvenir, about 54°S, Magallanes, Chile. *P. gayi* is found in steppes outside the forest habitat. Photo F. Vuilleumier, October 1987.

EXTRA-PATAGONIAN VICARIANCE

Twenty-six of 137 genera (19%) and 31 of 217 species (14%) have a pattern where the Patagonian species is replaced by one or more sister species outside of Patagonia. Several instances have been described (*Tinamotis*, Vuilleumier 1986; *Phalacrocorax*, Murphy 1936, Voisin 1973, Siegel-Causey 1988; *Charadrius*, Bock 1958; *Picoides*, Short 1975; *Muscisaxicola*, Vuilleumier 1971; *Anthus*, Murphy 1923, Hall 1961). The extra-Patagonian allospecies are elsewhere in South America (high Andes, *Tinamotis*; south-central South America, *Picoides*), the Falkland Islands (*Tachyeres*), North America (*Buteo*), islands of the Southern Ocean (*Phalacrocorax*), New Zealand (*Charadrius biceinctus*; Patagonian taxon is *falklandicus*, Bock 1958), and Central Asia (*Charadrius asiaticus*; Patagonian taxon is *modestus*, Bock 1958). I discuss below three cases representing a series from weak to strong morphological differentiation (Fig. 15).

(1) *Anas georgica* (family Anatidae) has populations in South America (*spinicauda*) and on South Georgia (*georgica*), about 1750 km E of Tierra del Fuego (Fig. 15). Murphy (1936) treated the South Georgian taxon as a species, but other authors (Watson 1975, Johnsgard 1978) consider South Georgian *georgica* a subspecies of *spinicauda*. I agree with Johnsgard (1978) that *georgica* and *spinicauda* are closely related to Old World *acuta*. A remarkable trait of the South Georgia isolate, which is resident, is its predilection for meat (Parmalee 1980), a food source not previously reported. Parmalee (1980) speculated that meat from carcasses represents an important food item during the harsh austral winter. South Georgia's *georgica* shows a food-niche shift, as well as a habitat shift, this duck living there in *Poa flabellata* tussock grassland, a habitat absent from the continent (but present in the Falklands).

(2) *Anthus antarcticus* (family Motacillidae) is the only land bird on South Georgia, where it is resident (Fig. 15). Murphy (1923) was baffled by its differentiation, finding *antarcticus* close to both *A. hellmayri* and *A. correndera* (but perhaps closer to *hellmayri*) and yet distinct from all species of South American *Anthus*. Hall (1961) considered *antarcticus* and *correndera* to be representative species, and further thought that *cor-*



FIG. 14. Top: *Nothofagus* forest, characteristic habitat of *Phrygilus patagonicus* on mainland near Rio Rubens, about 52°S, NW of Punta Arenas, Magallanes, Chile. *P. gayi* is found in steppes E of this forest habitat. Photo F. Vuilleumier, February 1987. Bottom: roadside second-growth scrub, uncharacteristic habitat of *P. patagonicus* on Navarino Island, about 55°S, Magallanes, Chile. *P. gayi* does not occur on Navarino Island. Photo F. Vuilleumier, November 1985.



FIG. 15: Schematic map to illustrate distribution and differentiation of taxa in the genera *Anas*, *Anthus*, *Melanodera*, *Nesospiza*, and *Rowettia* in South America, the Falkland Islands, South Georgia, Tristan da Cunha and Gough Island (see text).

rendera was possibly the representative of Old World *novaeseelandiae* (notice the parallel with *Anas georgica-spinicauda-acuta*). There seems little doubt that *antarcticus* is a full species, and that it originated from a South American ancestor similar to *correndera*, these two species being each others' closest relative (Watson 1975). The phylogeny of these two species and other South American — and other — pipits nevertheless awaits further study. Once more there is a habitat shift, *antarcticus* living in *Poa flabellata* grassland, a habitat absent from South America. In the Falklands, where *Poa flabellata* forms tussock grassland, *A. correndera* lives in other habitats (Pettingill 1973), namely in "exposed inland areas or heaths where white grass [*Cortaderia*] predominates . . . [and] . . . in areas where diddle-dee [*Empetrum*] is extensive." In southern South America, similarly, *A. correndera* lives in steppes, but there *Poa flabellata* tussock-grassland is lacking. Clapperton *et al.* (1989) wrote that "most of [South Georgia] was buried by a conterminous icecap during the last glacial maximum," and that the coast was ice-free "by at least 10,000 yr B.P." This would mean that colonization by *Anas* and *Anthus* could have occurred only since

about 10,000 years ago or more recently. In the case of *Anthus* this is a very short time for strong morphological divergence. This may be one of the best documented cases of the timing of allopatric speciation in birds.

(3) *Rowettia goughensis* (family Emberizidae) lives only on Gough Island in the South Atlantic, 4500 km from Cape Horn and 3200 km from Brazil (Fig. 15). This bunting is closely related to the Patagonian and Falkland genus *Melanodera* (Rand 1955, Watson 1975, Vuilleumier, unpubl. data). Greenway (1958) considered them congeneric, a treatment I would accept. Whether or not *Rowettia* and *Melanodera* are generically distinct, however, differentiation has gone one step further in this case than in that of *Anthus antarcticus*. (The bunting *Nesospiza*, from Tristan da Cunha [Fig. 15], is very close morphologically to both *Rowettia* and *Melanodera*. There is debate, however, whether *Nesospiza* is close to *Melanodera* phylogenetically.) Gough Island does not seem to have been glaciated in the Late Pleistocene. A pollen sequence dating back to about 40,000 years did not reveal floristic changes in this time span (Bennett *et al.* 1989, Gribnitz & Kent 1989). Thus, it appears

that Gough Island has been available for colonization for a much longer time than South Georgia, a fact that would help explain the much greater differentiation of *Rowettia* and *Melanodera* than that of *Anthus antarcticus* — *A. corren-dera*.

OVERLAPS

Eleven of 137 genera (8 %) and 25 species (12 %) present geographical and ecological overlaps. All cases are assumed to be the result of local speciation. The best studied instance is *Tachyeres* (Livezey 1986). In *Podiceps* (Storer 1982) and *Haematopus* (Jehl 1978) hybrids between overlapping species have been found. Sympatry is described in *Chloephaga* (Johnsgard 1978), *Thinocorus* (Maclean 1969), *Enicognathus* (Vuilleumier 1985), and *Muscisaxicola* (Vuilleumier 1971). The most complex case is *Chloephaga*, with broad sympatry and habitat co-occupancy between *picta* (commonest and most widespread species) and the two closely related species *poliocephala* and *rubidiceps*, whereas *hybrida* (closely related to *picta*) is ecologically allopatric and lives along the coast in the intertidal zone where kelp grows.

(Another species, *melanoptera*, occurs in the high Andes, and represents an instance of extra-Patagonian vicariance.) I discuss below one unpublished example in *Geositta*.

Geositta cunicularia (family Furnariidae) is widespread in the Andes and Patagonia, south to Tierra del Fuego across the Strait of Magellan, whereas its close relative *G. antarctica* has a very restricted range straddling the Strait of Magellan (Vaurie 1980) (Fig. 16). Scanty data in the literature suggest the two species have different habitat preferences in their overlap area, *cunicularia* occurring in grassy and *antarctica* in scrubby steppes. Recent research (Vuilleumier, unpubl. data) indicates a slight difference in habitat preference along a N-S gradient on the mainland, but nearly complete habitat overlap in NW Tierra del Fuego, where the two species live locally in mixed colonies (Fig. 17). At one study site on Tierra del Fuego, the two species of *Geositta* breed together, with their nests located as close as 20–30 m apart. Near the nesting sites, where small interspecific territories appear to be maintained, are feeding areas, where interspecific territoriality seems to break down, and where apparent mixed pairs forage for food. For both

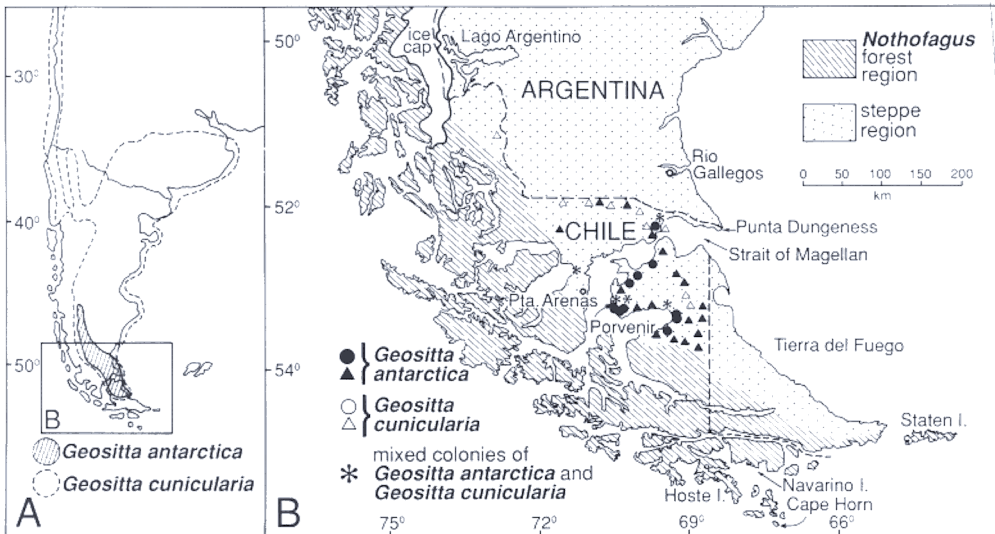


FIG. 16. A. Schematic map of the distribution of two overlapping sister species of steppe-dwelling *Geositta*. B. Distribution of *G. antarctica* and *G. cunicularia* in southern Patagonia, based on unpublished field work. Circles indicate specimens collected; triangles indicate observations. Although sympatric, the two species occur in mixed colonies only locally (indicated with *).



FIG. 17. Habitat of mixed colonies of *Geositta antarctica* and *G. cunicularia* E of Porvenir, about 53°S, Tierra del Fuego, Magallanes, Chile. Wet grassy meadow in foreground is feeding area; open scrubby steppe in background is breeding area. Photo F. Vuilleumier, October 1987.

species, and irrespective of whether they live together or not, suitable nesting habitat on that island consists of subterranean rodent colonies (*Ctenomys*), whether occupied or not by the mammals. The two *Geositta* species breed deep in rodent burrows (Fig. 18). Such habitat is patchily distributed in the steppes. Very little interspecific aggression takes place either near the nest holes or away from them. In the field the two species look very similar and behave in similar fashion, and at times are difficult to tell apart. Their vocalizations, however, are quite different. They are emitted quite often, and presumably serve as reproductive isolating mechanisms. Morphological differences (wing pattern; breast streaking; bill length), clearly detectable with specimens in hand, are actually somehow "minimized" in life, and foraging birds that do not call can occasionally be misidentified by visual means. No hybridization has been detected in the samples collected to date (about 65 specimens). Further studies of morphological and biochemical characters are in progress. Original vicariance might have taken place near the region of present overlap, perhaps in the Pleistocene. The distribution pattern suggests a double invasion, a phenomenon found in archipelagos.



FIG. 18. Top: *Geositta antarctica* at entrance of burrow. Bottom: excavated burrow; note three eggs at left; tape is about 1 m long. E of Porvenir, about 53°S, Tierra del Fuego, Magallanes, Chile. Photos F. Vuilleumier, October 1987.

RELICTS

Sixteen of 217 species (7%) in 14 of 137 genera (10%) can be considered relicts. These cases probably represent former local speciation, but extinction events have blotted out the clues to reconstructing vicariance and secondary events. The best studied taxa are *Pluvianellus* (Jehl 1975) and *Campephilus* (Short 1970). The other instances are described, but in less detail, by Johnsgard (1978, *Anas specularis*), Devillers (1977, *Larus scoresbii*), Vaurie (1980, *Eremobius*), Vuil-

leumier (1985, *Sylviorthorhynchus*, *Aphrastura*, *Pygarrhichas*, *Eugralla*, *Xolmis*, *Colorhamphus*, *Curaeus*; 1971, *Muscisaxicola*). One instance is unpublished (*Phrygilus*). Several of these genera are endemic to Patagonia (*Pluvianellus*, family uncertain; *Eremobius* [near-endemic], *Sylviorthorhynchus*, *Pygarrhichas*, three Furnariidae). Fig. 19 shows the distribution of two genera, *Pluvianellus* and *Eremobius*. There is debate about the generic status of *Eugralla*, which could be congeneric with *Scytalopus* (Vuilleumier 1985), and of *Colorhamphus*, which could be congeneric with *Ochthoeca* (Vuilleumier 1985) but which Lanyon (1986) prefers to keep as a monotypic

genus. There is no longer any discussion about *Leucophaeus scoresbii* belonging in *Larus* (Moynihan 1959, Devillers 1977), *Ipocrantor magellanicus* in *Campephilus* (Short 1970), or *Pyrope pyrope* in *Xolmis* (Vuilleumier 1971, Lanyon 1986).

The course of evolution is difficult to envision in these taxa, except perhaps *Larus*, if *scoresbii* is closely related to *belcheri*, which would suggest local speciation. In *Campephilus*, the origin of the Patagonian species can perhaps be traced to the time, early in the Cenozoic, when Patagonian forests were much closer to, if not in direct contact with, forests now separated by the arid diagonal stretching from the Pacific

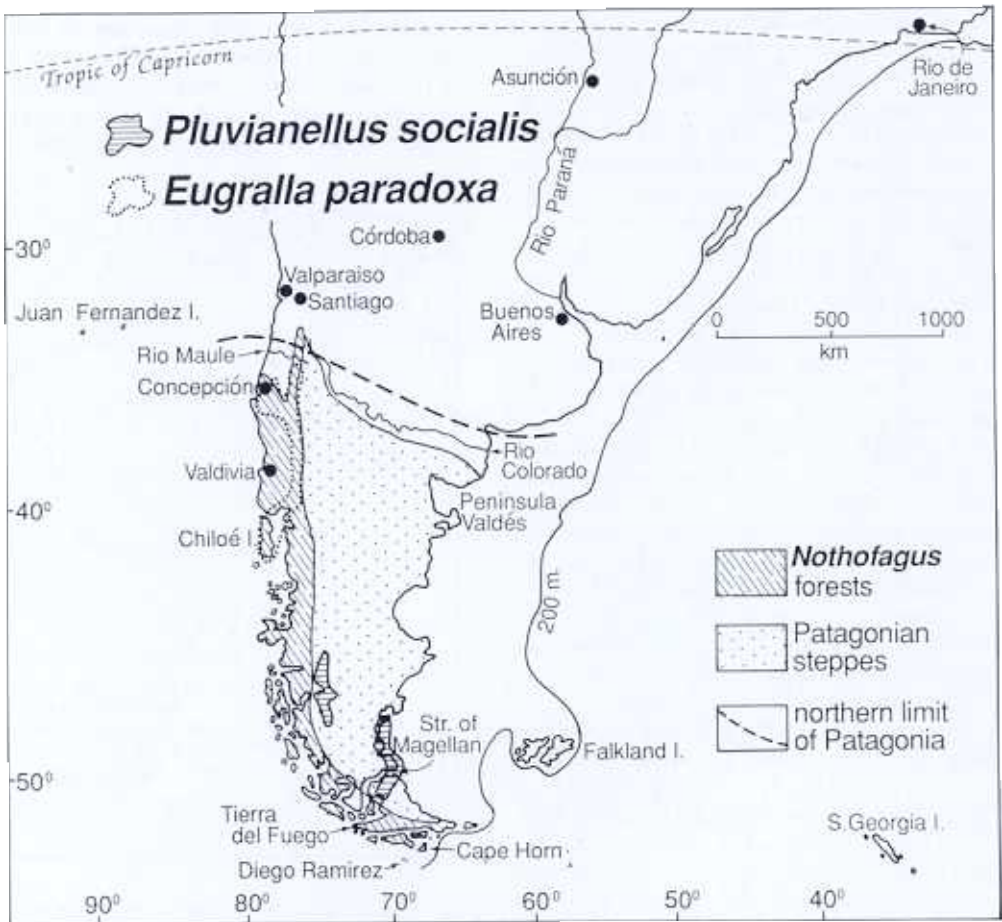


FIG. 19. Schematic map of Patagonia showing the distribution of two relict genera, *Pluvianellus* (horizontal lines) in steppes of southern Patagonia, and *Eugralla* (inside dotted line) in *Nothofagus* forests of northern Patagonia.

over the Andes to the Atlantic. In several instances the evolution of the relicts is linked to the history of *Nothofagus* forests (Vuilleumier 1985), but in other cases different habitats are involved (freshwater habitats for *Anas specularis*, lagoons and coastal areas for *Pluvianellus*, grassy steppes for *Muscisaxicola capistrata*). Patagonian taxa classified as relicts thus represent varied evolutionary histories, ranging in time from the Tertiary to the Pleistocene, and underscoring the complex changes, including vicariance, that affected all Patagonian habitats.

DISCUSSION

I now give preliminary answers to the three questions asked in the introduction.

(1) About a third of Patagonian species (73 of 217, or 34 %) show some evidence of speciation, from range disjunctions accompanied by weak differentiation, to parapatry and hybridization (*Catharacta*, *Phrygilus*), and to secondary range overlaps (*Geositta*). Vicariance events have therefore played an important role in the development of the Patagonian avifauna. Note that speciation has occurred across a broad taxonomic spectrum, from caracaras and ducks to furnariids and buntings. Whereas the occurrence of vicariance patterns and of overlaps implies the role of speciation or increase in species numbers, the occurrence of relicts suggests the role of extinction or loss of diversity. Thus my findings indicate that species numbers in Patagonia may be at an equilibrium between species enrichment through speciation and species decay through extinction. Some overlap patterns where interspecific interactions are weak (*Chloephaga*, *Geositta*) may represent the sort of cases studied by Cody (1974), in which "the whole genus behaves ecologically as a single species" (Cody 1970), a phenomenon worthy of further research.

(2) Vicariance events (barriers), as one can judge from present evidence, are or have been scattered geographically and ecologically in Patagonia. Some barriers are located in western Patagonia, others in the south, still others in the northwest. Both water and terrestrial birds show speciation. Finally, all trophic groups, from predators to insectivores and seedeaters, have been impacted by vicariance events. An analysis of barriers in Patagonia similar to the one I pub-

lished for Andean birds (Vuilleumier 1977) will be carried out in another publication.

(3) Pleistocene events have been so important in shaping the face of the modern Patagonian landscape that there can be little doubt that they also shaped the evolutionary history of its avifauna. Hence to attempt reconstructions such as Livezey (1986) did for *Tachyeres* is a justified endeavor. But clearly some of the patterns tabulated here (overlaps, relicts) refer to species which originated because of pre-Pleistocene vicariant events. Recent work by Ashworth (Ashworth & Markgraf 1989) on fossil beetles in cores of Late Pleistocene age show that these insects have had little evolutionary change over time. Ashworth (pers. comm.) thus suggested to me that whereas it was *reasonable* to infer speciation in birds within brief time intervals in the Pleistocene, in fact there was *no hard evidence* to indicate that our reconstructions of rapid change in birds are correct. Part of the problem, of course, is wheth-

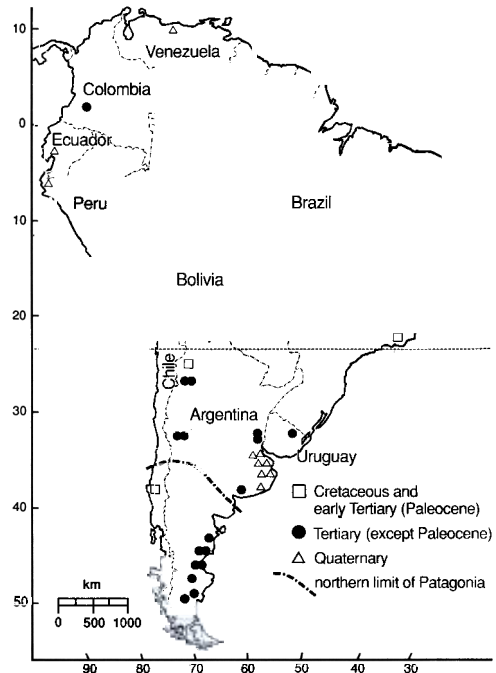


FIG. 20. Schematic map of South America showing the distribution of sites with fossil birds (redrawn from Rich 1979: 327). Note the large number of fossil sites in Patagonia.

er speciation events of an allopatric nature (vicariance) would be recorded in fossil assemblages. Some authors (Eldredge & Gould 1972, Gould & Eldredge 1977) would argue that vicariance events leading to speciation are so rapid that they leave no trace in the fossil record. Ashworth's remarks are nevertheless a salutary reminder that we must look for more evidence. Larry Marshall (pers. comm.) told me of numerous unstudied avian bones in southern Patagonian cave deposits. This is clearly one avenue of research (see Vuilleumier 1988: 1391), worth pursuing because Patagonia has many fossil sites from the Tertiary (Fig. 20). Another research strategy is to recreate past events on the basis of molecular differences.

Corbin *et al.* (1988) attempted just that, by correlating time and biochemical differentiation among *Tachyeres* populations. They assumed that the original vicariance event took place 60,000 years ago, then found good correlations between genetic distance values and time of divergence of various taxa. Unfortunately, there are no data to suggest exactly when that vicariance event took place. It is just as likely that the common *Tachyeres* ancestor was subjected to vicariance much earlier than 60,000 years ago. Although Corbin *et al.*'s (1988) reconstructions follow clear logic, lack of actual evidence suggests caution. Thus I cannot answer question (3). Many speciation events must have taken place in the Pleistocene (as in *Anthus*), but many others must have occurred much earlier. I do not know how many.

PROSPECT

My survey of speciation in Patagonian birds suggests a number of problems for further study. I list a few below.

(1) Can the actual barriers be identified and described in all or most vicariance cases? Does the localization of barriers form one or more patterns? Can these patterns be correlated with inferred paleoecological events? How widespread is hybridization between former isolates? Are there suture-zones in Patagonia? (*Sensu* Remington 1968: 322, defined as belts "of interfaunal and interfloral linkage".)

(2) How do the species behave toward each other in areas of secondary overlap? Is interspecific territoriality common?

(3) What is the nature of reproductive isolation in parapatric zones?

(4) What can Pleistocene-Holocene avian fossils teach us about the speciation history of Recent Patagonian birds?

To date, very few detailed analyses have been carried out on speciation in Patagonian birds. In view of the fact that speciation phenomena are so widespread in this region, there is need for a concerted effort at global study. The genera *Chloephaga*, *Haematopus*, *Charadrius*, *Asthenes*, *Pteroptochos*, *Anthus* and *Melanodera*, would seem especially good target taxa for detailed interdisciplinary research. I suggest also that ornithologists work closely with paleobotanists and paleozoologists (Ashworth & Markgraf 1989, COHMAP members 1988) in trying to decipher the history of their favorite creatures.

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