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Karyotypic polymorphism and evolution within and between the *Liolaemus monticola* (Iguanidae) "northern 2n = 38-40" chromosome race populations in central Chile

Polimorfismo cromosómico y evolución intra e inter poblacional de la raza cromosómica "Norte 2n = 28-40" de *Liolaemus monticola* (Iguanidae) en Chile Central

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ABSTRACT

Chromosomal genotypes were scored from 359 *Liolaemus monticola* lizards of the "northern, 2n = 38-40" chromosomal race from 21 locality samples between the Maipo (and one of its tributaries) and the Aconcagua (and one of its tributaries) ribers, plus a sample from the interracial hybridization zone, and some representative locality samples of the "southern 2n = 34" and the "multiple fission 2n = 42-44" chromosomal races for comparisons. The first seven variable chromosomal pairs were coded as Mendelian genotypes and statistically summarized by several clustering and population genetic algorithms. Spatial and temporal differentiation was assessed by chromosome frequencies, chromosomal diversity and heterozygosity. While no differentiation was found for diversity in the "northern 2n = 38-40" race, chromosomal frequencies and heterozygosity showed significant spatial differentiation that permit distinguishing between the coastal, Andean and transversal mountain range populations. The sample of Cuesta Chacabuco may represent a hybrid zone between the other two range samples. The origin of the chromosomal rearrangements, the population cytogenetics, and the recombination patterns resulting from chromosomal heterozygosity are compared in these chromosomal races, thus expanding the geographical area. These patterns are discussed with respect to the evolution of this complex in Chile and the importance of the riverine barriers in central Chile.

Key words: Iguanidae, *Liolaernus monticola,* chromosomal races, "northern 2n = 38-40" chromosomal race, population structure, speciation.

RESUMEN

Se cuantificaron los "genotipos" cromosómicos para 359 lagartijas de 21 muestras poblacionales de la raza "Norte, 2n = 38-40" comprendida entre los ríos: río Maipo y uno de sus afluentes el río Yeso y río Aconcagua (y uno de sus afluentes el río Juncal). Con fines comparativos agregamos una muestra de la zona de hibridación interracial, algunas muestras representativas de la raza "Sur 2n = 34" y una de la raza "múltiples fisiones 2n = 42-44". Los siete primeros pares cromosómicos variables fueron codificados como genotipos mendelianos y resumidos en varios algoritmos de agrupaciones y de genética de poblaciones. La diferenciación espacial y temporal fue pesquisada por las frecuencias cromosómicas, la diversidad cromosómica y la heterocigocidad. Si bien en la raza "Norte 2n = 38-40" no encontramos diferenciación para la diversidad cromosómica, las frecuencias y la heterocigosidad cromosómicas muestran una significativa diferenciación espacial, permite distinguir las poblaciones procedentes de la cordillera de La Costa, cordillera de Los Andes y cordón transversal. La muestra Cuesta de Chacabuco (Transversal) podría corresponder a una zona de hibridación entre los restantes rangos. La comparación entre las razas cromosómicas en relación al origen de los rearreglos cromosómicos, a la citogenética poblacional y a los patrones de recombinación genética resultantes de la heterocigosidad, permiten expandir el área de estudio y discutir la evolución de este complejo en Chile, destacando la importancia de algunas barreras biogeográficas como los ríos de Chile Central.

Palabras clave: Iguanidae, *Liolaemus monticola,* razas cromosómicas, polimorfismo cromosómico, estructura poblacional, especiación.

INTRODUCTION

Karyotypic polymorphism in natural populations has attracted the attention of evolutionary biologists since the 1940s, in part because of the detailed studies of Dobzhansky and co-workers on *Drosophila.* In Chile, Prof. Danko Brncic and collaborators conducted extensive and relevant studies examining inversions in several *Drosophila* species, endemic of Chile and South America, and showed that many of these revealed different temporal and spatial patterns of chro-

mosomal polymorphism (Dobzhansky 1962, 1970, Brncic 1969, 1970, 1976, 1985). They distinguished between "rigid" and "flexible" polymorphisms in *Drosophila.* In the first type, the frequencies of different chromosomal rearrangements do not change with latitude, altitude, season or temperature, but the second type the frequencies do change with the aforementioned factors.

Karyotypic polymorphisms have also been documented in other animal taxa involving several different classes of chromosomal rearrangements (White 1978a, 1978b, King 1981, 1993). One of the classes is the Robertsonian polymorphisms found in rodents, such as *Mus musculus* (Capanna 1980), *Spalax ehrenbergi* (Wahrman et al. 1969), and in the lizards *Sceloporus grammicus* (Hall & Selander 1973, Sites, 1983, Sites & Moritz 1987, Sites et al. 1987, Arévalo et al. 1991), and *Liolaemus monticola* (Lamborot 1991,1993, 1998, Lamborot & Alvarez-Sarret 1989, 1993, Lamborot et al. 1979, 1981). However, factors responsible for the maintenance of some polymorphisms in natural populations are still poorly understood.

Liolaemus monticola von Müller & Helmich (1932) is a highly variable, endemic montane lizard species distributed along the temperate mountain Ranges in Chile, between latitudes 30° and 40° S and at altitudes between 900 and 2,300 m (Donoso-Barros 1966, Peters & Donoso-Barros 1970). Two of the three *L. monticola* subspecies karyotyped previously (Lamborot et al. 1979, 1981), *L. m. villaricensis* and *L. m. chillanensis* from the southern part of the range (39° and 37° S), retain a relatively conservative diploid chromosomal pattern of 2n = 32, with 12 macrochromosomes and 20 microchromosomes, considered ancestral in *Liolaemus* (Lamborot 1991, 1993, Lamborot & Alvarez-Sarret 1981, Lamborot et al. 1979, 1981, 1989) and other iguanids (Gorman 1973, Paull et al. 1976). The third subspecies, *L. monticola monticola,* displays a latitudinal gradient of karyotypic diversity and complexity (Lamborot 1993). At present, we can distinguish the "primitive 2n = 32", the "southern 2n = 34", the "northern 2n = 38 to 40" and the "multiple mission 2n = 40 to 44 (MF)" (Lamborot 1998). These chromosomal races differ primarily in macrochromosomal number because of centric fissions. More complex rearrangements, including translocations, pericentric inversions, enlarged chromosomes and increase in microchromosome pairs, have also been reported in this species (Lamborot 1998). Elsewhere, we (Lamborot 1991, 1993, Lamborot & Alvarez-Sarret 1993) hypothesized that the "northern race" is derived from the "southern 2n = 34"; these races are clearly separated by the Maipo river from the high Andes to the Pacific coast (Lamborot 1991, Lamborot & Alvarez 1993). Hybridization between the races is, however, found only in a narrow zone south of the Yeso river, and a tributary of the Maipo river near Santiago (Lamborot 1991, 1993). A second river barrier, the Aconcagua separates the "northern" and the "multiple mission (MF)" chromosomal races (Lamborot 1988, Lamborot unpublished results). These results suggest that these rivers have contributed to the formation and morphological differentiation of these races (Lamborot & Eaton 1992, 1997, Lamborot et al. 1999, and unpublished results), by interrupting gene flow between the populations.

This paper concentrates on chromosomal differentiation within the "northern 2n = 38-40" chromosomal race populations. The aims are: (i) to review previous data on chromosomal polymorphism within and between the "northern 2n = 38-40" chromosomal race, adding several new localities and samples; (ii) to map the distribution of these populations to establish their spatial relationships; (iii) to estimate the frequencies and distributions of within sample polymorphisms and to compare with Hardy-Weinberg expectations; and (iv) for some samples to assess the temporal relationships; (v) to examine the basis of the polymorphisms, and conduct between-site frequency studies within the geographical distribution of the races; (vi) to compare the genetic distances with the morphological (Lamborot & Eaton 1992, 1998) and chromosomal differentiation (Lamborot 1991, 1993, Lamborot & Alvarez-Sarret 1989) previously obtained; and vii) to compare the polymorphism in pair 3 in the northern race populations plus the MF race and the Yeso Sur sample. The Yeso Sur location represents a zone of secondary contact between the southern and the northern races with interracial hybrids, and samples are included from this site to address the following questions: (i) Are there chromosomal differences between demes within each year, and are these differences consistent over the chromosomal frequencies? (ii) are the patterns of demic differentiation consistent over years?, and (iii) considering the total chromosome frequency of each deme, is there a tendency towards spatial homogenization of genetic structures over the years? These may give clues about the factors involved in the chromosomal population structure and the maintenance of polymorphisms.

MATERIAL AND METHODS

Study area and sampling

All *L. monticola monticola* were collected from spring to autumn, in 27 localities. The geographical range of the *L. monticola* "northern 2n = 38 to 40" race extends from between the Maipo and the Yeso rivers in the south to the Aconcagua and Juncal rivers in the north, at altitudes from 650 to 1,850 m, and covers about 500 km^2. Some of these localities had been sampled previously. With the individuals collected, a total of 359 lizards have been scored for karyotypes. Thus, "northern" race lizards were from Andean (samples 12 to 18, in the Appendix, Fig. 1), coastal (samples 2 to 4, 6 to 9) and transversal mountain ranges (sample 11 from Cuesta de Chacabuco). The transversal range is located between the coastal and the Andean range. Other localities represented by fewer than 7 lizards were not considered. Figure 1 shows the geographic locations sampled for this study (see also the Appendix, and Table 1). Representative samples from the "southern 2n = 34 race" (from El Volcán Sur and Los Queñes, 200 km south of

TABLE 1

Chi-square for deviation from Hardy-Weinberg equilibrium in all *Liolaemus monticola* samples with polimorphism in chromosome 3, with 1 degree of freedom

Chi cuadrado para desviaciones al equilibrio de Hardy-Weinberg en todas las muestras de las poblaciones de *Liolaemus monticola* con polimorfismo en el cromosoma 3, con un grado de libertad

Population sample	Expected class	Observed frequency	Expected frequency	X^2	P	Population sample	Expected class	Observed frequency	Expected frequency	X^2	P
1 Roble	A-A	0	0.53	0.059	0.808	13 Arrayán	A-A	1	1.44	0.297	0.59
	A-B	2	1.89				A-B	7	6.12		
	B-B	8	8.05				B-B	5	5.44		
2 Roble 90	A-A	2	0.51	5.75	0.017	14 Farellones 80	A-A	5	5.14	0.015	0.901
	A-B	4	6.98				A-B	10	9.73		
	B-B	22	20.51				B-B	4	4.14		
3 CamRob92	A-A	1	0.84	0.053	0.817	15 Farellones 91	A-A	5	5.87	0.508	0.476
	A-B	5	5.32				A-B	14	12.26		
	B-B	7	6.84				B-B	5	5.87		
4 Rungue92	A-A	2	1.41	0.45	0.502	16 Yerba Loca 90	A-A	3	2.44	0.369	0.543
	A-B	7	8.18				A-B	6	7.11		
	B-B	11	10.41				B-B	5	4.44		
5 Dormida88	A-A	1	0.84	0.053	0.817	17 Manzano	A-A	1	1.47	0.394	0.530
	A-B	5	5.32				A-B	6	5.05		
	B-B	7	6.84				B-B	3	3.47		
6 Dormida90	A-A	2	0.35	10.75	0.001	18 Lagunillas	A-A	0	0.77	1.667	0.197
	A-B	1	4.31				A-B	5	3.46		
	B-B	12	10.35				B-B	2	2.77		
7 Dormida94	A-A	0	0.00	0.00	1.00	19 San Alfonso	A-A	3	4.12	1.184	0.276
	A-B	1	1.00				A-B	11	8.76		
	B-B	10	10.00				B-B	3	4.12		
8 Dormida96	A-A	2	0.68	3.713	1.00	20 San Gabriel	A-A	5	5.51	0.143	0.705
	A-B	4	6.63				A-B	16	14.98		
	B-B	15	13.68				B-B	9	9.51		
9 Dormida98	A-A	1	0.80	0.079	0.779	21 Yeso Norte	A-A	1	1.90	1.314	0.252
	A-B	6	6.40				A-B	7	5.21		
	B-B	11	10.80				B-B	2	2.90		
10 Campana	A-A	1	0.84	0.053	0.817	22 Yeso Sur	A-A	25	23.53	1.488	0.223
	A-B	5	5.32				A-B	13	15.94		
	B-B	7	6.84				B-B	4	2.53		
11 Cta Chacabuco	A-A	4	3.59	0.118	0.731	27 Mina Hierro Viejo	A-A	0	0.97	1.425	0.233
	A-B	12	12.83				A-B	11	9.07		
	B-B	11	10.59				B-B	18	18.97		
12 Saladillo	A-A	3	2.67	0.089	0.765						
	A-B	11	11.67								
	B-B	12	11.67								

the other populations), and from the coast (Cerro Cantillana), are also included here. I also examined lizards from Yeso Sur, which is considered as a zone of secondary contact of the "northern" X "southern" 2n = 34 race, and which is characterized by the production of hybrids as the previously described from a sample of 26 lizards. Finally, I included a sample of the "multiple fission" (2n = 42-44) race and from Mina Hierro Viejo (previously described by Lamborot 1988) as an outgroup (locality 27 in Fig. 1; also see Table 1 and the Appendix).

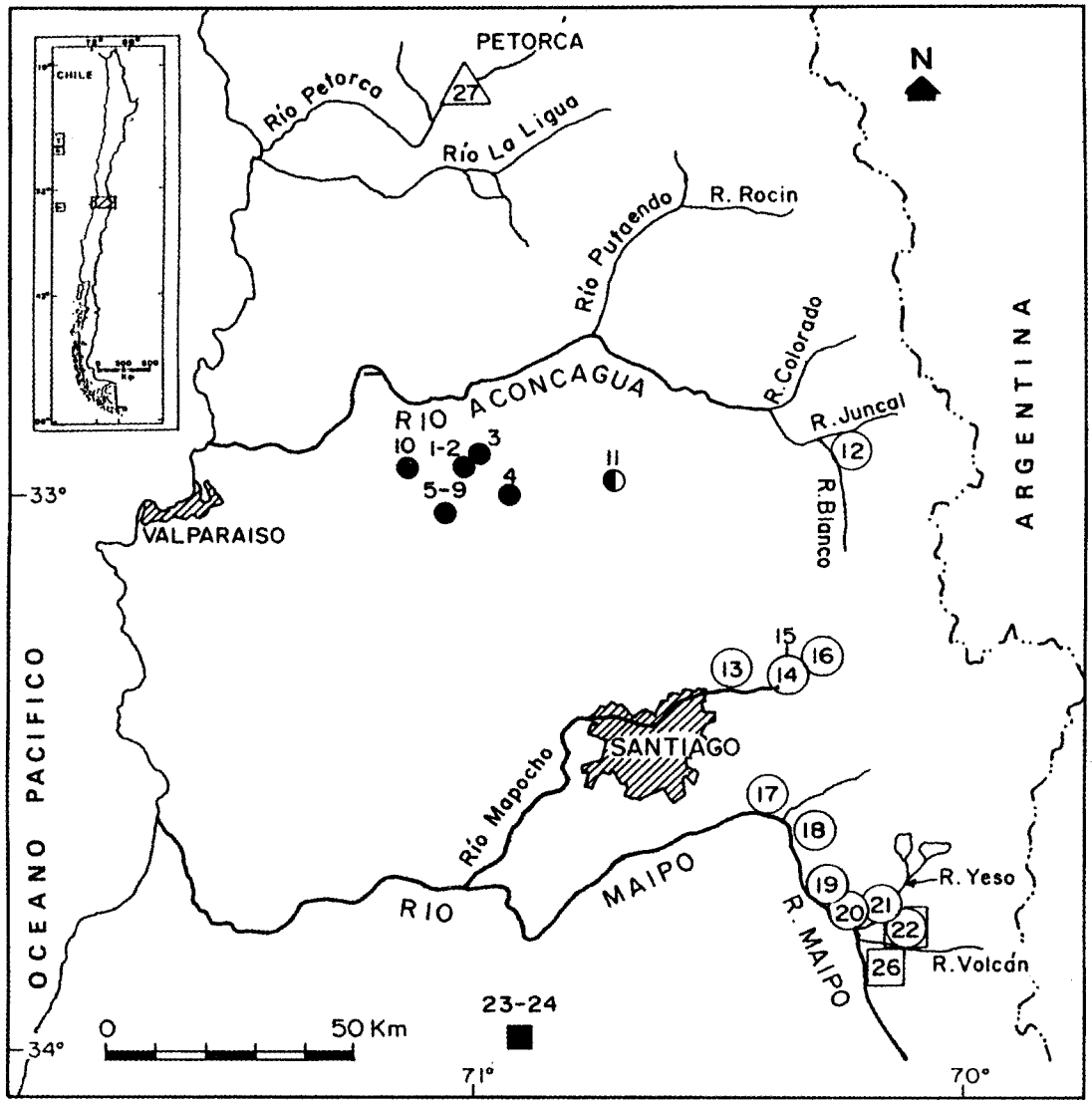

Fig. 1. Map of the distribution and location of the cytotypes of 27 sample sites and the chromosomal races of *Liolaemus monticola* identified across a part of central Chile, on the basis of the UPGMA clustering algorithrns. The numbers correspond to the localities sampled for the chromosomal analysis (Table 5). Symbols identify particular races and ecodemes: Squares: southern race; circles : northern race; triangles: multiple fission race. Solid symbols: coastal deme; empty symbol: Andean ecodeme; half solid half empty: transversal ecodeme; circle inside the square: the hybrid zone. Sample locality 25 (Los Queñes) is not shown on the map; it is about 200 km south of the Maipo river.

Mapa de distribución y ubicación de los citotipos en 27 muestras de las razas cromosómicas de *Liolaemus monticola* identificadas en una parte de Chile Central basado en algoritmos de agrupación. Los números corresponden a las muestras de las localidades para los análisis cromosómicos (Tabla 5). Los símbolos identifican las razas cromosómicas y ecodemos: cuadrados: raza sur; círculos: raza norte; triángulos: raza múltiple fisiones. Símbolos sólidos: demos costeros. Símbolos vacíos: ecodemo andino; mitad sólido y mitad vacío: ecodemo transversal. Círculo dentro de cuadrado: zona de hibridación interracial. No figura la localidad de Los Queñes (25) que se encuentra a 200 kms del sur del río Maipo.

Chromosome preparation and interpretation of karyotypes

Standard karyotypes were obtained from bone marrow, liver, spleen and testes, using the colchicine-hypotonic pretreated air-drying treatment (Evans et al. 1964), and stained with Giemsa. At least six selected somatic metaphase and meiotic plates from each specimen were analyzed and photographed to score the chromosomal "genotypes". We followed the abbreviations of Arévalo et al. (1991) and Lamborot (1998) to describe the morphology ("genotypes") of the macrochromosomal complement, and the first microchromosome pair 7 (Fig. 2). The ancestral biarmed non-fission chromosome morphology was called "A", and the simple fission rearrangements "B". Inversions of the ancestral biarmed chromosomes were coded as "C", whereas inversions of the fission product in chromosome pair 2 were noted as "D". The enlarged chromosome was noted as "E", and chromosome fusions were noted as "F". Additional observations of spermatocytes at diakinesis, showing chiasmata and metaphase II complements, were also included when available, for confirmation of these interpretations.

Statistical analyses

The coded genotypes were analyzed by using the BIOSYS-1 program (Swofford & Selander 1981). The frequencies of all chromosomal rearrangements were calculated for all samples (Table 1). An UPGMA dendrogram based on genetic distances (Nei 1972, 1978, Rogers 1972) was generated with BIOSYS-1, and the exact formula of Levene for small samples was used to calculate expected values fide Li (1955). I also plotted groups of samples into more inclusive units, "ecodemes", to denote particular mountain ranges: coastal, transvesal or Andean; or "genodemes" ("metademes") to denote a particular genotype frequency. Multiple regression was then used to test for association of the fission frequency in pair 3, using the STAT package. To assess temporal variation in frequencies of chromosomal polymorphisms, two or more years were analyzed for three different sites of the "northern 2n = 28-40" race from the coastal range: cerro El Roble (1984, 1990), cuesta La Dormida (1988, 1990, 1994, 1996, 1998), and from the Andean range: camino a Farellones (1980, 1991).

Voucher specimens are deposited in the collection of the Cytogenetics Laboratory, Facultad de Ciencias, Universidad de Chile. Each specimen from which chromosomes were examined is designated by its individual catalog number (L N°) of the laboratory.

RESULTS

Chromosomal race karyotypes

The southern 2n = 34 race. This race presents six pairs of metacentric or submetacentric macrochromosomes and 22 microchromosomes (Lamborot 1991, Lamborot & Alvarez-Sarret 1993), but in this sample four of forty lizards from the Cantillana coastal range (locality 23-24 in Fig. 1) were heterozygous. These animals all shared a rearrangement that I interpreted as a fusion of chromosomes 5 and 7, scored as AF (2n = 33, Fig. 2). This chromosomal rearrangement was only found in this locality.

The northern race 2n = 38 to 40. This race differs from the "southern race" by the fixed fission condition in pair 4 and the high frequency of the pair 3 fission polymorphism (Fig. 2), plus one pair of microchromosomes (thus 24 microchromosomes) in both sexes. In all the karyo-

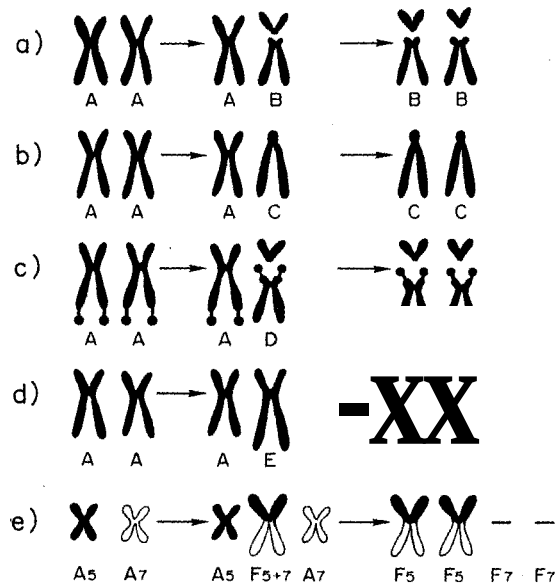

Fig. 2. Diagrammatic representation of the chromosomal rearrangement derivation sequences with the genotype codes for any given pair of macrochromosomes and microchromosomal pair 7, based on inferred chromosomal rearrangements.

Diagrama representativo de las secuencias de derivación de los rearreglos cromosómicos con los códigos genotípicos para cualesquier par de macrocromosomas incluyendo el par 7 de microcromosomas, en base a los rearreglos inferidos.

types the pair 4 biarmed macrochromosome is replaced by four acrocentric chromosomes (Fig. 2), and all possible combinations of chromosomal polymorphisms expected for the macrochromosome pair 3 fission were found. Some lizards were homozygous for two metacentric macrochromosomes (St3F4, scored as AA, 2n = 38, Fig. 2), some were heterozygous for one metacentric plus two acrocentrics (P3F4, scored as AB, 2n = 39, Fig. 2); and some were homozygous for the pair 3 acrocentric (F3F4, scored as BB, 2n = 40). One fissioned product of chromosome 3 showed a subtelocentric instead of acrocentric morphology, and this chromosome was used as a marker for the fissioned pair 3b.

The hybrid zone. The northern (2n = 38-40) X southern (2n-34) contact zone at Yeso Sur (Lamborot 1991) was sampled again after a road construction that altered the original site studied in 1983. From a sample of 42 lizards, 15 were chromosomally "pure southern" genotypes, 12 were "pure northern" lizards, and the remaining 15 lizards appeared to be hybrids (Appendix).

The multiple fission (MF) 2n = 42-44 race. The karyotypes were previously reported by Lamborot (1998); this race retains the same chromosomal features as the northern race, but is characterized by several new chromosomal polymorphisms: (i) a pair 1 fission (genotype scored as "B"); (ii) a pair 2 fission plus a pericentric inversion in one of the fission products, which shifts the NOR and satellite from the tip of the long arm of the submetacentric pair 2 to the short arm of the fission product (scored as "D", Fig. 2); (iii) an enlarged chromosome pair 6 (scored as "E"); and (iv) a polymorphism for a pericentric inversion in pair 7 (scored as "C", Fig. 2). This race is distributed north of the Aconcagua river (Lamborot 1998).

TABLE 2

Provenance of 22 *Liolaemus monticola*, "northern, 2n = 38-40" sample populations and distance from a hypothetical refuge locality (0,00 km) in the coastal mountain range. Latitude and longitude in min

Procedencia de 22 muestras de poblaciones de la raza "Norte 2n = 38-40" de *Liolaemus monticola* y su distancia desde un refugio hipotético (0,00 km) en el rango de la cordillera de la Costa. Latitud y longitud en min

Sample and location	Year	Fission pair 3 frequecy	Latitude S	Longitude W	Altitude (m)	Distance from a coastal range refugee (km)
1 El Roble	1985	0.900	1.978'	4.261'	1,400	93.0
2 El Roble	1990	0.857	1.978'	4.261'	1,400	93.0
3 Cam a El Roble	1992	0.731	1.979'	4.260'	690	84.0
4 Rungue-Caleu	1992	0.725	1.980'	4.257'	690	85.0
5 Cta Dormida	1988	0.731	1.983'	4.262'	1,300	72.0
6 Cta Dormida	1990	0.833	1.983'	4.262'	1,300	72.0
7 Cta Dormida	1994	0.955	1.983'	4.262'	1,300	72.0
8 Cta Dormida	1996	0.810	1.983'	4.262'	1,300	72.0
9 Cta Dormida	1998	0.778	1.983'	4.262'	1,300	72.0
10 Cº Campana	1990	0.731	1.977'	4.267'	1,400	87.0
11 Cta Chacabuco	1994	0.630	1.978'	4.243'	1,100	107.5
12 Cam a Saladillo	1996	0.673	1.977'	4.217'	1,450	148.5
13 Arrayán	1990	0.654	2.000'	4.228'	1,400	205.0
14 Cam Farellones	1980	0.474	2.001'	4.222'	1,400	195.0
15 Cam Farellones	1991	0.500	2.001'	4.222'	1,400	195.0
16 Yerba Loca	1990	0.571	1.999'	4.220'	1,800	200.0
17 El Manzano	1991	0.600	2.015'	4.224'	1,350	220.0
18 Lagunillas	1986	0.643	2.017'	4.220'	1,500	233.0
19 San Alfonso	1979	0.500	2.023'	4.218'	1,106	243.0
20 San Gabriel	1981	0.567	2.026'	4.214'	1,250	250.0
21 Yeso Norte	1985	0.550	2.027'	4.212'	1,320	256.0
22 Yeso Sur*	1991	0.250	2.027'	4.213'	1,300	118.25
27 Hierro Viejo	1991	0.810	1937'	4.260'	350	———

* Plus others years

Population cytogenetics

Population structure: hierarchical analysis. Table 5 summarizes the coded genotypes scored for *Liolaemus monticola* in central Chile, and their distributions are shown in Fig. 1. The genotype frequencies for the seven chromosome pairs were used to calculate genetic distance and similarity coefficients, and these were clustered to produce a dendrogram (Fig. 3), which provided easy visualization of the distinct groups.

The population samples showed no significant deviation from the frequencies of the heterozygotes and homozygotes expected under Hardy-Weinberg equilibrium at chromosome pair 3 (Table 1), except three samples (No. 2, 6 and 8) of the northern race from the coastal range. At chromosome pair 4, the P4 hybrids (sample No. 22) from the hybrid zone, were statistical deficient. In general, the coastal range samples exhibited lower heterozygote P3 frequencies, and differed significantly ($P < 0.04$) from Hardy-Weinberg ratios when all populations were combined (Table 3). Samples of the "northern race" from the Andean range were in equilibrium, although most of them presented more observed heterozygotes than the expected. When all samples of the "northern race" from the Andean range

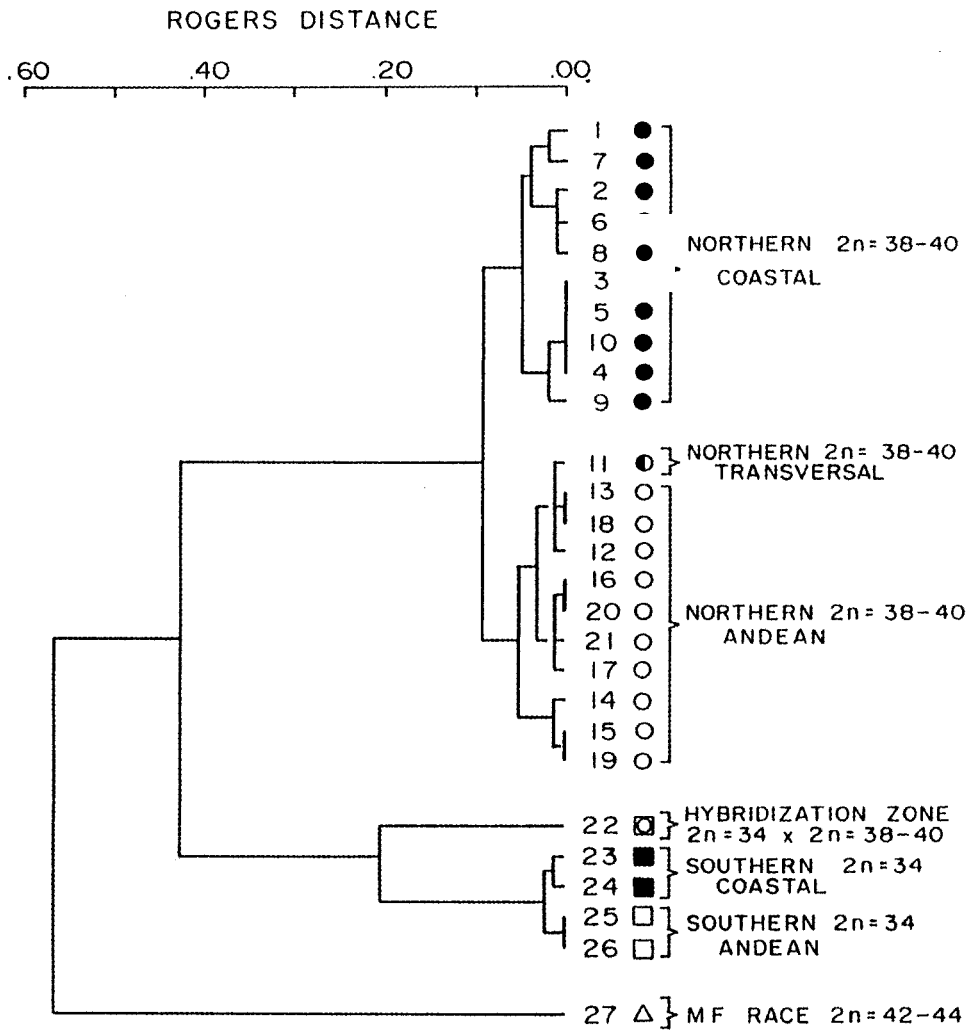

Fig. 3. Dendrogram based on Rogers' genetic distance values for all pairwise comparisons of 27 *Liolaemus monticola* samples (numbers identifies localities and year of collection, see Appendix, Table 5 and Fig. 1).

Dendrograma basado en los valores de las distancias genéticas de Rogers para todas las comparaciones en pares de las 27 muestras de *Liolaemus monticola* (los números identifican las localidades y año de recolección, ver Tabla 5 del Anexo y Fig. 1).

TABLE 3

Comparison of the observed (O) and the expected (E) Hardy-Weinberg equilibrium values of pair 3 fission polymorphism in four localities that represent all samples of the coastal and the Andean northern race plus the transversal, the hybridization zone, and the multiple fission race of *L. monticola*

Comparación de los valores observados (O) y esperados (E) en el equilibrio de Hardy-Weinberg para el polimorfismo de fisión del par 3 en cinco localidades de *Liolaemus monticola* que representan todas las muestras de la raza "Norte 2n = 38-40" costeras, andinas, del cordón transversal, más la zona de hibridación (Yeso Sur) y la raza "múltiples fisiones 2n = 42-44"

Sample and locality	Homozygotes St_3 St_3		Heterozygotes St_3 F_3 (P_3)		Homozygotes F_3 F_3		X^2	P	Fixation index (F)	FF *
Coastal range	O	12	O	40	O	110	8.206	0.004	0.221	0.802
n = 162	E	6.24	E	51.52	E	104.24				
Transversal range	O	4	O	12	O	11	0.118	0.731	0.047	0.630
n = 27	E	3.59	E	12.83	E	10.59				
Andean range	O	27	O	93	O	50	2.117	0.145	-0.115	0 .568
n = 170	E	31.66	E	83.69	E	54.66				
Yeso Sur	O	25	O	13	O	4	1.488	0.223	0.175	0.250
n = 42	E	23.53	E	15.94	E	2.53				
Hierro Viejo	O	0.0	O	11	O	18	1.425	0.223	- 0.235	0.810
n = 29	E	0.97	E	9.07	E	18.97				

FF = frequency of fission

were combined, and all from the coastal, and these compared with the transversal range, and the hybridization zone, and the "multiple fission race" (Table 3), only the ecodeme from the coastal range exhibited statistically deviation for a deficiency in P3 heterozygotes. The ecodeme from the Andean range showed a slight excess of heterozygotes, but this excess was not statistically significant (P = 0.145) from Hardy-Weinberg expectations.

Diversity and heterozygosity. Following Crow & Kimura (1970) I estimated the allelic diversity at a "gene locus" (chromosome) by the effective number of "alleles" (chromosomal rearrangements). In the 27 localities the heterozygosity increased with the latitudinal position of the chromosomal races. The "southern race" from the Andean region has no polymorphic loci, populations from the coastal range (Cerro Cantillana) have two, based on a single low frequency reciprocal fusion event, the "northern race" with one fixed and one polymorphic locus, and finally the MF race has five polymorphic loci.

Table 4 shows the hierarchical F-statistics (F_{IS}, F_{IT}, and F_{ST}) for: (i) the "northern 2n = 38-40 race" in the coastal range, (ii) the Andean range, (iii) the transversal mountain range, (iv) the hybridization zone (sample of Yeso Sur), and (v) the "MF 2n = 42-44 race" (sample of Mina Hierro Viejo). The negative F_{IS} values correspond to a non significant value for an excess of heterozygotes in the chromosomal pairs 1 and 2 of the MF race. The mean values F_{IS} for all samples show a small increase of heterozygotes; F_{ST} indicates that chromosomal variation between demes within a race and between the races is greater (52.8 %) than within the demes.

TABLE 4

Summary of the F-statistics at all loci (chromosomes) for the same *Liolaemus monticola* samples to those of Table 3

Resumen de los estadígrafos F de Wright para todos los loci (cromosomas) para las mismas muestras de *Liolaemus monticola* que figuran en la Tabla 3

"Locus" chromosome	F (IS)	F (IT)	F (ST)
Pair 1	- 0.094	0.885	0.895
Pair 2	- 0.074	0.909	0.915
Pair 3	0.015	0.188	0.176
Pair 4	0.327	0.658	0.492
Pair 6	0.367	0.606	0.377
Pair7	0.306	0.436	0.188
Mean	0.127	588	528

Level of within-population and within the ecodemes of the "northern 2n-38-40" race

When we only analyze the polymorphism in pair 3 for all the "northern race" samples they maintain similar levels of genetic variation. But within this race the observed heterozygosities were generally statistically less than in the Coastal samples, or greater than, but very close to, the Hardy-Weinberg expected heterozygosities in the Andean samples, in spite of the small sample sizes. Due to the similar frequency within each deme, coastal and Andean, we grouped the samples in ecodemes (Table 3). In those few cases, however, fixation indexes were generally positive, indicating a deficiency of heterozygotes only the coastal range value was significantly different from zero.

Spatial and temporal chromosomal variation. In general, the most important aspect is that the pair 3 polymorphism persists through time at similar frequencies, often for a span of several years (Fig. 4). We statistically evaluated the temporal changes in the pair 3 fission frequencies using a replicated goodness of fit test (G statistic, Sokal & Rohlf 1981), and the results show that there were no significant differences. I therefore pooled the samples collected in different years from the same locality for further analysis.

Figure 5 depicts the correlation between all samples with latitude that clearly separated the

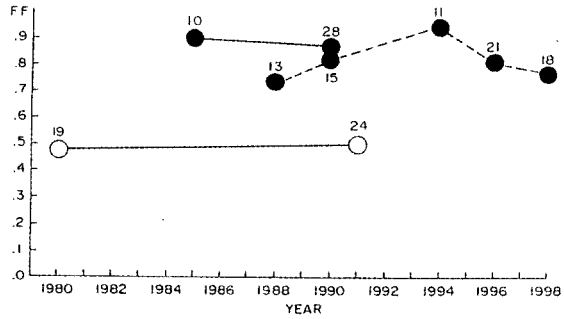

Fig. 4. Variation in the chromosomal fission pair 3 frequencies (vertical axis) for three populations of the *Liolaemus monticola* northern race, 2n = 38-40 from which samples were taken in more than one year (year of collection on horizontal axis). Solid circles, coastal range: Cerro El Roble (solid line) and Cuesta La Dormida (discontinued line); empty circles, Andean range: Farellones. Numbers correspond to sample size for each year.

Variación de la frecuencia de fisión del par 3 (eje vertical) en tres poblaciones cuyas muestras fueron tomadas en más de un año (año de recolección en el eje horizontal). Círculos sólidos, cordón Costero: cerro El Roble (línea sólida) y cuesta La Dormida (línea discontinua); círculos vacíos: cordón Andino: camino a Farellones. Los números indican el tamaño de la muestra, para cada año.

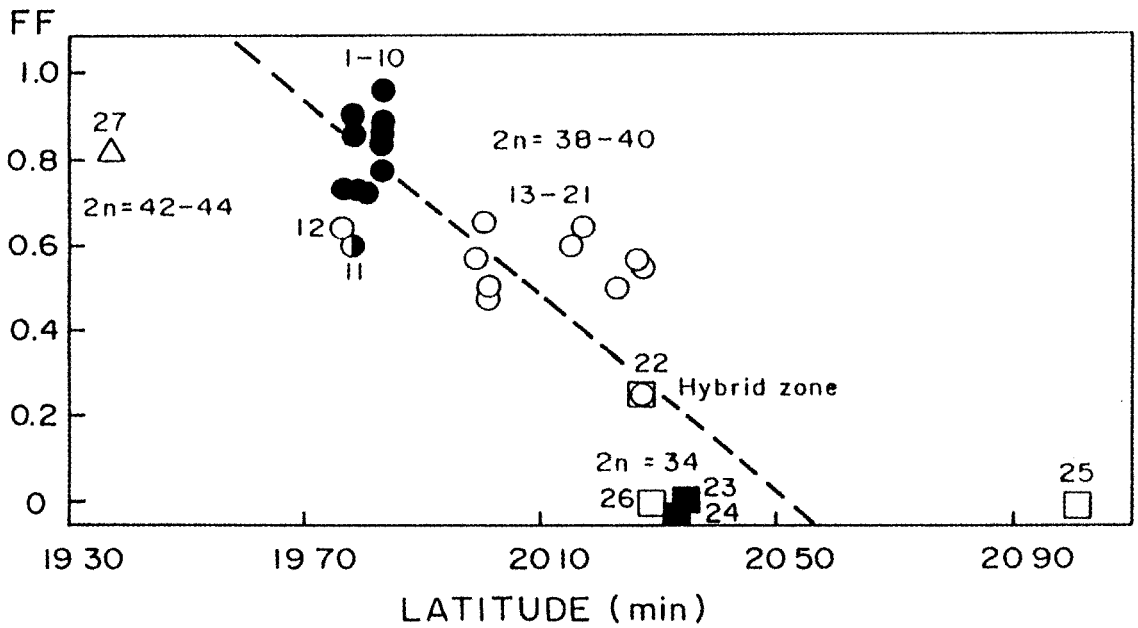

Fig. 5. Frequency for the fission in pair 3 in the 27 *Liolaemus monticola* samples against latitude in min. The symbols are the same as in Fig. 1.

Frecuencia de la fisión del par 3 en 27 muestras de *Liolaemus monticola* en relación a la latitud en min. Los símbolos corresponden a los de la Fig. 1.

TABLE 5

Locality, sample size (n), and chromosomal "genotype" analized by BIOSYS-1 for all lizards of *Liolaemus monticola* chromosomal races examined in this study. The seven "loci" explained in the Introduction correspond to the first 7 pair of chromosomes. Samples are in the Appendix

Localidad, tamaño de muestra (n) y "genotipo" analizados mediante BIOSYS-1 de lagartijas de las razas cromosómicas de *Liolaemus monticola* examinadas en este estudio. Los siete "loci", correspondientes a los primeros 7 pares cromosómicos se explican en la Introducción. Las muestras figuran en el Apéndice

		Chromosome pair "genotype"									Chromosome pair "genotype"						
Sample	n	1	2	3	4	5	6	7	Sample	n	1	2	3	4	5	6	7
1 Cerro El Roble	0	AA	AA	AA	BB	AA	AA	AA	10 Cerro La Campana	1	AA	AA	AA	BB	AA	AA	AA
1985 1,400 m	2	AA	AA	AB	BB	AA	AA	AA	1,400 m	5	AA	AA	AB	BB	AA	AA	AA
	8	AA	AA	BB	BB	AA	AA	AA		7	AA	AA	BB	BB	AA	AA	AA
2 Cerro El Roble	2	AA	AA	AA	BB	AA	AA	AA	11 Cuesta Chacabuco	4	AA	AA	AA	BB	AA	AA	AA
1990 1,400 m	4	AA	AA	AB	BB	AA	AA	AA	1,100 m	12	AA	AA	AB	BB	AA	AA	AA
	22	AA	AA	BB	BB	AA	AA	AA		11	AA	AA	BB	BB	AA	AA	AA
3 Camino al Roble	1	AA	AA	AA	BB	AA	AA	AA	12 Camino a Saladillo	3	AA	AA	AA	BB	AA	AA	AA
1992 750 m	5	AA	AA	AB	BB	AA	AA	AA	1,450 m	11	AA	AA	AB	BB	AA	AA	AA
	7	AA	AA	BB	BB	AA	AA	AA		12	AA	AA	BB	BB	AA	AA	AA
4 Entre Rungue y Caleu	2	AA	AA	AA	BB	AA	AA	AA	13 El Arrayán	1	AA	AA	AA	BB	AA	AA	AA
1992 700 m	7	AA	AA	AB	BB	AA	AA	AA	1,400 m	5	AA	AA	AB	BB	AA	AA	AA
	11	AA	AA	BB	BB	AA	AA	AA		7	AA	AA	BB	BB	AA	AA	AA
5 Cuesta La Dormida	1	AA	AA	AA	BB	AA	AA	AA	14 Camino a Farellones	5	AA	AA	AA	BB	AA	AA	AA
1988 1,300 m	5	AA	AA	AB	BB	AA	AA	AA	1980 1,450 m	10	AA	AA	AB	BB	AA	AA	AA
	7	AA	AA	BB	BB	AA	AA	AA		4	AA	AA	BB	BB	AA	AA	AA
6 Cuesta La Dormida	2	AA	AA	AA	BB	AA	AA	AA	15 Camino a Farellones	5	AA	AA	AA	BB	AA	AA	AA
1990 1,300 m	1	AA	AA	AB	BB	AA	AA	AA	1991 1,450 m	14	AA	AA	AB	BB	AA	AA	AA
	12	AA	AA	BB	BB	AA	AA	AA		5	AA	AA	BB	BB	AA	AA	AA
7 Cuesta La Dormida	0	AA	AA	AA	BB	AA	AA	AA	16 Yerba Loca 1990	3	AA	AA	AA	BB	AA	AA	AA
1994 1,300 m	1	AA	AA	AB	BB	AA	AA	AA	1,800 m	6	AA	AA	AB	BB	AA	AA	AA
	10	AA	AA	BB	BB	AA	AA	AA		5	AA	AA	BB	BB	AA	AA	AA
8 Cuesta La Dormida	2	AA	AA	AA	BB	AA	AA	AA	17 El Manzano	1	AA	AA	AA	BB	AA	AA	AA
1996 1,300 m	4	AA	AA	AB	BB	AA	AA	AA	1,350 m	6	AA	AA	AB	BB	AA	AA	AA
	15	AA	AA	BB	BB	AA	AA	AA		3	AA	AA	BB	BB	AA	AA	AA
9 Cuesta La Dormida	1	AA	AA	AA	BB	AA	AA	AA	18 Camino a Lagunillas	0	AA	AA	AA	BB	AA	AA	AA
1998 1,300 m	6	AA	AA	AB	BB	AA	AA	AA	1,500 m	5	AA	AA	AB	BB	AA	AA	AA
	11	AA	AA	BB	BB	AA	AA	AA		2	AA	AA	BB	BB	AA	AA	AA

TABLE 5 (cont.)

Sample	n	1	2	3	4	5	6	7
19 San Alfonso	3	AA	AA	AA	BB	AA	AA	AA
1979 1,106 m	11	AA	AA	AB	BB	AA	AA	AA
	3	AA	AA	BB	BB	AA	AA	AA
20 San GabrieL	5	AA	AA	AA	BB	AA	AA	AA
1981 1,250 m	16	AA	AA	AB	BB	AA	AA	AA
	9	AA	AA	BB	BB	AA	AA	AA
21 Yeso Norte	1	AA	AA	AA	BB	AA	AA	AA
1985 1,350 m	7	AA	AA	AB	BB	AA	AA	AA
	2	AA	AA	BB	BB	AA	AA	AA
22 Yeso Sur	15	AA	AA	AA	AA	AA	AA	AA
1991 1,300 m	3	AA	AA	AA	BB	AA	AA	AA
	6	AA	AA	AB	BB	AA	AA	AA
	3	AA	AA	BB	BB	AA	AA	AA
	7	AA	AA	AA	AB	AA	AA	AA
	1	AA	AA	BB	AB	AA	AA	AA
	6	AA	AA	AB	AB	AA	AA	AA
	1	AA	AA	AB	AA	AA	AA	AA
23 Cerro Cantillana	19	AA	AA	AA	AA	AA	AA	AA
1988 1,500 m	1	AA	AA	AA	AA	AF	AA	AF
24 Cerro Cantillana	36	AA	AA	AA	AA	AA	AA	AA
1990 1,500 m	3	AA	AA	AA	AA	AF	AA	AF
25 Los Queñes 1,400 m	39	AA	AA	AA	AA	AA	AA	AA
26 El Volcán Sur 1,415 m	12	AA	AA	AA	AA	AA	AA	AA

Sample	n	1	2	3	4	5	6	7
27 Mina Hierro Viejo 350 m	6	BB	DD	BB	BB	AA	AA	AA
	4	BB	DD	AB	BB	AA	AA	AA
	2	BB	DD	BB	BB	AA	AE	AA
	2	BB	DD	AB	BB	AA	EE	AC
	1	BB	DD	BB	BB	AA	EE	AA
	2	AB	DD	BB	BB	AA	EE	AA
	2	BB	DD	BB	BB	AA	AE	AC
	1	BB	DD	BB	BB	AA	AE	CC
	1	AB	DD	BB	BB	AA	AE	AA
	1	AB	DD	AB	BB	AA	AA	AA
	1	BB	DD	AB	BB	AA	EE	CC
	1	BB	DD	AB	BB	AA	EE	AA
	1	AB	AD	BB	BB	AA	AE	AC
	1	BB	AD	AB	BB	AA	AE	AA
	1	BB	AD	BB	BB	AA	AA	AC
	1	BB	AD	BB	BB	AA	EE	AC
	1	BB	DD	AB	BB	AA	AE	CC

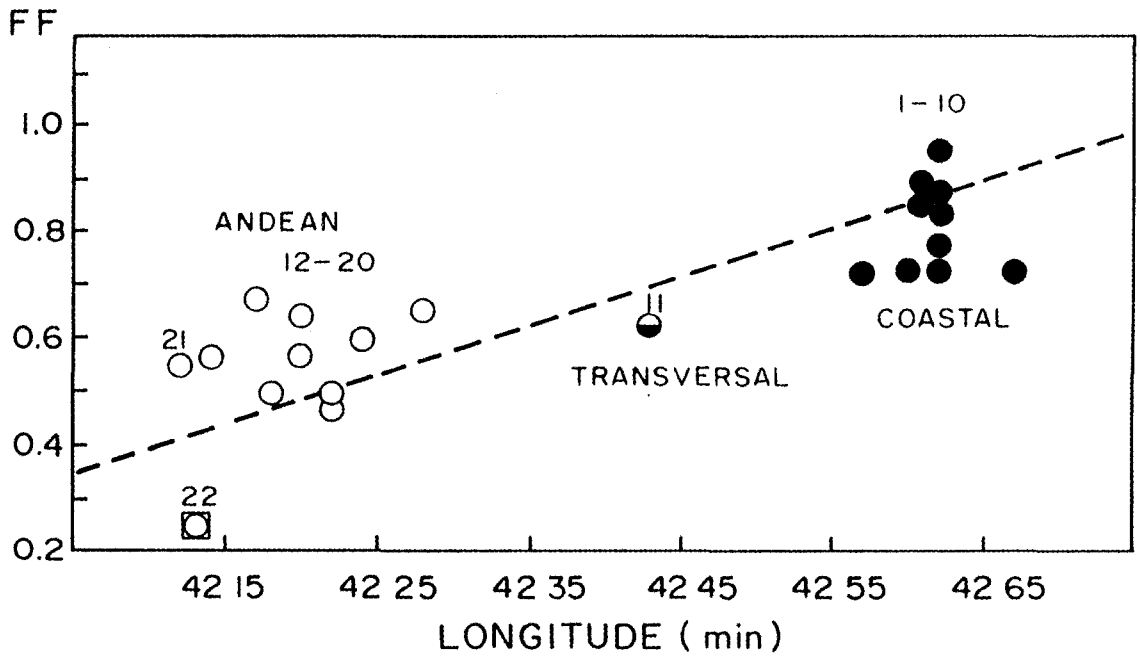

Fig. 6. Frequency for the fission in pair 3 in the *Liolaemus monticola* "northern 2n = 38-40" chromosome race samples against longitude. The symbols are the same than in Fig. 1.

Frecuencia de la fisión del par 3 en las muestras de la raza "Norte 2n = 38-40" de *Liolaemus monticola* en relación a la longitud en minutos. Los símbolos corresponden a los de la Fig. 1.

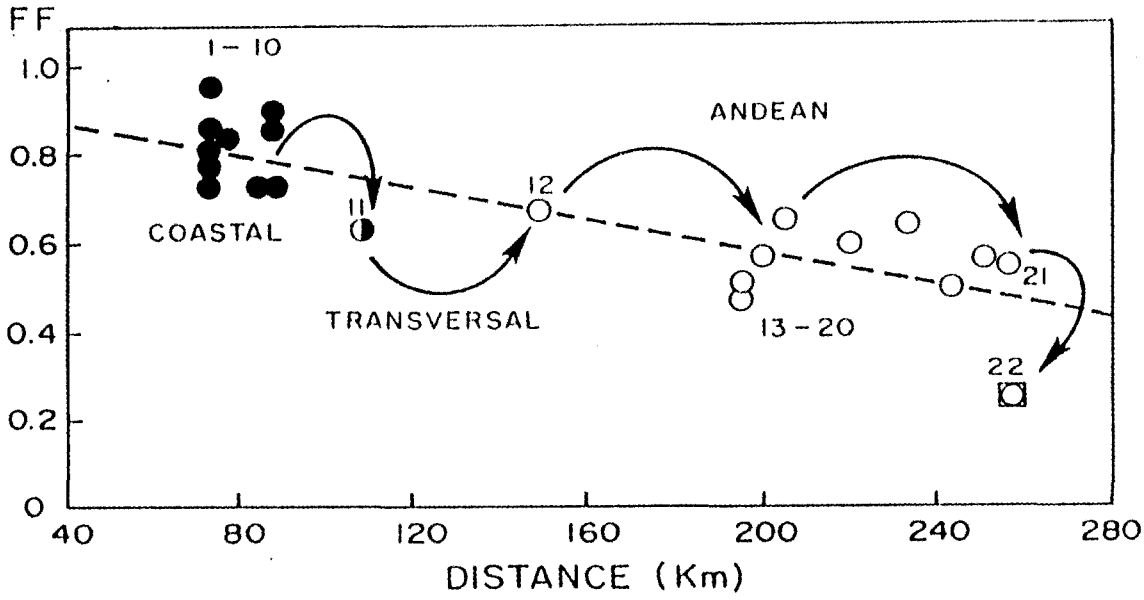

Fig. 7. Frequency for the fission in pair 3 in the *Liolaemus monticola* "northern 2n = 38-40" chromosome race against the distance in km from a hypothetical refugee in the coastal range. The symbols are the same than in Fig. 1.

Frecuencia de la fisión del par 3 en las muestras de la raza "norte 2n = 38-40" de *Liolaemus monlicola* en relación a la distancia en km desde un refugio hipotético en el rango costero. Los símbolos corresponden a los de Fig. 1.

"southern", and the "northern" races, the Andean and coastal ranges except for two samples: 11 Cuesta Chacabuco and 12 Saladillo that respectively belong to the transversal and to the Andean ranges. Similar results are found with longitude for all "northern race" population samples including sample 22 from the hybrid zone (Fig. 6), and in relation to the distance in kilometers from hypothetical refuge (Fig. 7).

DISCUSSION

Geographical and chromosomal aspects

The addition of several new localities to those previously described in Lamborot (1991, 1993, 1998) and Lamborot & Alvarez-Sarret (1993) confirms and extends our earlier findings in several ways. The basic karyotype that characterizes the "northern 2n = 38-40" race populations analyzed is now expanded to include the area between the Maipo river, south to the Yeso river (a tributary), north to the Aconcagua river (and one of its tributaries, the Juncal river); this area is approximately 500 km^2. The altitudinal range for this race extends from 650 m (in the Coastal range) to 1,950 m, which is wider than the previously reported (Donoso-Barros 1966, Peters & Donoso-Barros 1970, Lamborot et al. 1979, Lamborot 1991, 1993, Lamborot & Alvarez-Sarret 1993).

The dendrogram depicted in Fig. 3 identifies three distinct groups corresponding to the three chromosomal races: (i) "northern", (ii) "southern", and (iii) "multiple fission". This distributional pattern is in agreement with the geographical and topological features of central Chile, which includes riverine barriers. Within the "northern race" I can further distinguish two subgroups; (i) those of the Andean, and (ii) those of the coastal range (based on P3 chromosomal frequencies). The Cuesta Chacabuco lizards from the transversal range appear genetically "intermediate" between the Andean and coastal ranges, which is also suggested by their geographic location.

The northern 2n = 38-40 chromosomal race. All included samples of this race attain a frequency of 100 % for the fixed acrocentrics in pair 4. Among the important factors determining the pair 4 fixation are the mutation rate and the degree of heterozygote disadvantage, and the population structure. A high level of aneuploidy in the hybrids P4 from the hybrid zone at the Yeso Sur locality (Lamborot & Alvarez-Sarret 1993) suggests that negative heterosis may be a factor in hybrid fitness. This disadvantage has also been shown for the P3 chromosomal rearrangement with medium a level of aneuploidy amounting 10 to 23 % in the coastal range, or may be extremely heterotically negative in the hybrids from the hybridization zone (Lamborot 1993). This contrasts with the P3 of the Andean range, present in a nearly neutral state (Lamborot 1993).

One global advantage for the acrocentric condition for the fissioned pair 4, was advanced by Lamborot (1993), via a reduced chiasma count in the spermatocyte bivalents. In most of the *Liolaemus monticola* populations with nonfissioned macrochromosomes (as the "southern" race), the observed chiasmata are invariably interstitial and distal. In contrast, the "southern 2n = 34", "northern 2n = 38-40" races and the hybrids from the Yeso Sur locality show recombination patterns that differ statistically from each other (Lamborot & Alvarez-Sarret 1993). Also, it is possible that chromosomal recombination in the derived "northern race 2n = 38-40" being affected by the increase in the number of chromosomal pairs due to the fissioning process. This means an increase in the number of linkage groups, allowing independent recombination, but limiting recombination to chiasmata at the end of the chromosomal segments, preserving blocks of gene sequences that may represent mechanisms for maintaining particularly adaptive gene linkage groups.

The fission pair 3 polymorphism is present in all localities of the "northern" race as well as the "MF" sample, but the frequencies of this polymorphism differ between these races. Further, the frequencies in the pair 3 fission appear to persist through time within the populations, but differences among localities and between races be partially explained by meiotic aspects (Lamborot, 1993).

Rigid versus flexible polymorphism. The fission frequencies in the polymorphic pair 3 of the "northern 2n = 38-40" race were statistically different when we compare the Andean versus Coastal mountain ranges. This suggests that selection responds more readily to local environmental variation than mating systems and dispersal mechanisms. If true, then pair 3 fission frequencies may track environmental gradients while remaining constant within each region. This interpretation is consistent with spatial and temporal comparisons showing that pair 3 frequency differentiation in time is much less marked than in space. This must serve as tentative evidence for a metapopulation structure characterized by the interplay between locally differential selection for viability and fertility and moderate dispersal abilities. Population genetic selection theories

predict that this strategy is very effective in maintaining genetic polymorphisms and thus adaptability.

¿How can the pair 3 polymorphism be explained? One simplest model is that this local karyotypic variation may largely have arisen many thousands of years ago, when the typical population structure of the *Liolaemus monticola* may have been very different from that observed now. One possibility is that the polymorphism represents the "ghost of hybridization past". There are a number of ways in which past hybridization events may generate long-lasting polymorphisms. In particular, a polymorphism may be generated following a colonization process similar to that envisaged for the house mice where the initial range expansion of *Mus musculus* into Sweden is thought to have involved descendants of individuals from the north German section of the hybrid zone between *Mus musculus musculus* and *M. musculus domesticus* (Gyllensten & Wilson 1987, Prayer et al. 1993). The *L. monticola* chromosomal race "2n = 38-40" that initially colonized and replaced the bulk of the current "southern race 2n = 34", north from the Maipo river, ultimately fixed the fissioned pair 4, but left the Robertsonian polymorphism for fission in the chromosome pair 3 that has become very widespread. The fact that such polymorphism may have persisted for many thousands of years after the range expansions is compatible with single simple heterozygotes suffering only slightly reduced fertility relative to homozygotes. The reduced fertility estimated by Lamborot & Álvarez-Sarret (1993), demonstrated that the amount of aneuploidy found in the heterozygotes lizards P3F4 from the "northern race" in the coastal range is greater than the levels for both homozygotes, and this contrasts with the lower frequency of aneuploidy from the P3F4 lizards in the Andean range outside the hybrid zone (Lamborot 1991) or, pair 3 represents an ancestral polymorphism that has been sorted into geographic patterns of frequency variation by selection in different environments.

The approaches to explain the Robertsonian polymorphism P3 external to hybrid zones in *L. monticola* "northern" chromosomal race, the stochastic events like chance colonization events or chance mutations in the origin of the polymorphism has been emphasized, with the small selection against the P3 heterozygotes in the coastal range, contrasting with a possible small selection favoring the P3 at the Andean range and in both ranges large population size determining its persistence. Clearly, then the P3 Robertsonian polymorphism in *L. monticola* "northern race" must be considered external to the hybrid zone. At least three general models can explain this polymorphism: past hybridization events, de novo mutation and natural selection. Those models that have been formulated not only have relevance with regards to the understanding of the Robertsonian polymorphisms in *Liolaemus,* and specially *Liolaemus monticola,* they also reflect a wide range of possibilities with regards to the colonization history of the species and have implications with regards to the initial fixation of Robertsonian acrocentrics.

Possible route of migration and/or colonization. In previous studies based on chromosomal (Lamborot 1993) and on morphological analyses (Eaton & Lamborot 1992, 1997) we hypothesed that the "northern race" is derived from the "southern race", probably in the coastal range, both in the Maipo valley and in the Aconcagua Valley, that escaped the action of the Pleistocenic glaciers (Brüggen 1950, Huesser 1966, Vuilleumier 1971, Caviedes 1972, Formas 1979), and the glacial tongues may well have acted as greater barriers in the Andean than in the coastal mountain range. In the present day the rivers Maipo, Yeso, Aconcagua, and Juncal act as a barrier to the gene flow. Then the species crossed to the Andes using the transversal range as a bridge, and only later reached the Andes north of the Maipo river. In our results on the morphological variation the greater differences between the "southern" and the "northern" races were in the Andes. When the fission pair 3 frequency was plotted against longitude or the distance in kilometers (Fig. 6 and 7) from an hypothetical refuge in the coastal range (Table 2) the P3 frequency tended to decrease with both the increased distance in kilometers or longitude in minutes. In spite of this, sample 11 (Cuesta de Chacabuco) from the transversal range, deserves a special mention because we do not believe that the polymorphisms listed in Tables 1 and 5, may be external to current hybrid zone. The high level of P3 resembles more to the Andean range populations, based on the high frequency of the P3 lizards and the H-W equilibrium. In spite of this, in our preliminary meiotic and mitotic survey a percentage of aneuploidy for the acrocentric products is high and higher than those P3 of the Coastal range previously analyzed (Lamborot & Alvarez-Sarret 1993). In previous studies (Lamborot & Eaton 1992, 1997) the multivariate analysis of meristic characters among samples was sufficient to differentiate the chromosomal races, and also distinguishes populations of the coastal range from those of the Andes with the Cuesta Chacabuco sample intermediate; a possible historical sequence of events that accounts

for the pattern of morphological differentiation was advanced (Lamborot & Eaton 1992, 1997). Also they confirmed the Maipo and the Yeso rivers as riverine barriers, and preliminary results from electrophoresis indicates that this sample seems to correspond to an intermediate population sample between the coastal and Andean samples (M. Lamborot umpublished results).

The multiple fission (MF) race. The MF race diploid number ranges from 2n = 42 to 44 chromosomes; all variants retain the same characteristics described for the "northern" race plus the polymorphism condition for the fissioned macrochromosome pairs 1 and 2, plus a pericentric inversion in one of the fissioned product of chromosome 2, plus a polymorphism for an enlarged chromosome pair 6 and for a pericentric inversion in chromosome pair 7. Those aspects were discussed in Lamborot (1998). Because the MF race retains the fixation of the macrochromosome pair 4 fission, and the pair 3 fission polymorphism and it exhibits the same number of microchromosomes, this race may be considered derived from the "northern race". The frequency of the P3 heterozygotes is in equilibrium according to Hardy-Weinberg.

Chromosomal evolution. One of the main goals of interest in a species as variable as *Liolaemus monticola* is the possible link between the huge chromosomal variation and speciation. The linear arranged karyotypic variation with an increased complexity from south to north, is in several aspects concordant with the Hall's "cascade model of speciation" (Hall 1973, 1980, 1983) or the "chain process" (White 1978) or King's "primary chromosomal allopatry" (King 1981). Some of the chromosomal races differ by fixed chromosomal rearrangements when compared between the "primitive, 2n = 32" considered ancestral in *Liolaemus* and the "southern 2n = 34" whose fixed differences correspond to a reciprocal translocation between chromosome pair 5 and 7 that change the size and shape in both chromosome plus the addition of one microchromosome pair. Then the "northern 2n = 38-40" race retains this fixed rearrangements and adds the fixed pair 4 centric fission and is polymorphic for the fission in pair 3, plus the addition of another pair of microchromosomes. Also, a narrow zone of secondary contact was detected. Then the "MF 2n = 42-44" race, retains the same chromosome features of the "northern 2n = 38-40" race, but adds the polymorphic conditions aforementioned in the chromosome pairs 1 and 2, 6 and 7.

At present there is a variety of models for chromosome speciation and along with many problems (see King 1981, Sites 1983, Sites & Moritz 1987, 1993, Sites & Reed 1994). I will postpone a more detailed discussion in another paper, when more evidences on chromosomal data, new chromosomal races and molecular genetic data had been obtained.

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APPENDIX 1

List of the karyotyped lizards identified by the Laboratory Catalog numbers of the Laboratorio de Citogenética, Facultad de Ciencias, Universidad de Chile (in parentheses) and locality data used in this study

Lista de lagartos con cariotipos, utilizados en este estudio, de acuerdo a la identficación del número de Catálogo (en paréntesis) del Laboratorio de Citogenética, Facultad de Ciencias, Universidad de Chile y datos sobre las localidades

I.- The "northern 2n = 38-40" chromosome race from:

(A) The coastal mountain range: Cerro El Roble (32° 58'S, 71° 00' W). 1- 1985 at 1350-1500m: P_3F_4: 2 males (L-966; 975). F_3F_4: 3 males (L-967; 970; 971); 5 females (L-968; 969; 972; 973 ; 977). 2- 1990 at 800-1650 m: St_3F_4: 2 males (L-1581; 1582). P_3F_4: 2 males (L- 1479; 1580); 2 females (L-1480 ;1572). F_3F_4: 12 males (L-1560-1565; 1570; 1571; 1576-1579); 10 females (L-1566-1569; 1573-1575; 1583; 1584a; 1584b). 3- Camino al Roble (32° 59' S, 71° 01' W). 1992 at 700-850 m: St_3F_4: 1 male (L- 2010). P_3F_4: 1 male (L-2009); 4 females (L-2012; 2014; 2016; 2018). F_3F_4: 5 males (L-2008; 2013; 2017; 2019; 2020); 2 females (L- 2011; 2015). 4- De Rungue a Caleu. (33° 00' S, 70° 58' W, lat.700-800 m). 1992: St_3F_4: 2 males (L-2032; 2037). P_3F_4: 5 males (L-2034; 2035; 2039; 2041; 2045); 2 females (L-2033; 2043). F_3F_4: 6 males (L-2027; 2029-2031; 2038; 2042); 5 females (L-2028; 2036; 2040; 2044; 2046). 5- Cuesta La Dormida (33° 02' S, 71° 03' W) at 1300-1400 m: 1988: St_3F_4: 1 male (L-1104). P_3F_4: 3 males (L-1097; 1101; 1131); 2 females (L-1106; 1106b). F_3F_4: 3 males (L-1098; 1100; 1132); 4 females (L-1095; 1096; 1099; 1105). 6- 1990: St_3F_4: 2 females (L-1408; 1455). P_3F_4: 1 male (L-1407). F_3F_4: 8 males (L-1400-1403; 1406; 1450; 1451; 1456); 4 females (L-1409; 1410; 1452; 1453). 7- 1994: P_3F_4: 1 male (L-2146). F_3F_4: 3 males (L-2147; 2154; 2223); 7 females (L-2148-2150; 2155-2157; 2224). 8- 1996: St_3F_4: 1 male (L-2533); 1 female (L-2487). P_3F_4: 4 males (L-2488; 2489; 2525; 2531). F_3F_4: 6 males (L-2493; 2523; 2524; 2532; 2534; 2535); 9 females (L-2491; 2492; 2494; 2495; 2526; 2527; 2528; 2529; 2530). 9- 1998: St_3F_4: 1 female (L-2692). P_3F_4: 3 males (L-2696; 2697; 2701); 3 females (L-2688 ;2689 ;2691). F_3F_4: 3 males (L-2695; 2699; 2700); 8 females (L-2687; 2690; 2693; 2702-2706). 10- Cerro La Campana (32° 57' S, 71° 08' W, altitude 1350-1500 m. 1990: St_3F_4: 1 male (L-1381). P_3F_4: 1 male (L-1382); 4 females (L-1386-1389). F_3F_4: 4 males (L-1383; 1384; 1391; 1392); 3 females (L-1385; 1390; 1393).

(B) The transversal mountain range: 11- Cuesta de Chacabuco (32° 58' S, 70° 42' W, altitude 1000-1200 m). St_3F_4: 2 males (L- 2213; 2221); 2 females (L-2084; 2212). P_3F_4: 7 males (L-2079; 2080; 2082; 2086; 2215; 2219; 2220), 5 females (L-2087; 2209-2211; 2217). F_3F_4: 6 males (L-2078; 2081; 2083; 2214; 2216; 2278); 5 females (L-2085; 2218; 2279-2281). C- The Andean mountain range: 12- Saladillo (32° 55' S, 70° 10' W, altitude 1400-1500 m).1996: St_3F_4: 2 males (L-2453; 2454); 1 female (L-2286). P_3F_4: 4 males (L-2289; 2449; 2452; 2467); 7 females (L-2447; 2451; 2457; 2458; 2460; 2463; 2465). F_3F_4: 8 males (L-2287; 2288; 2290; 2448; 2450; 2456; 2468; 2475); 4 females (L- 2455; 2459; 2466; 2474). 13- El Arrayán (33° 20' S, 70° 28' W, altitude 1300-1500 m). St_3F_4: 1 female (L-1092). P_3F_4: 3 males (L-1091; 1439; 1448); 4 females (L-1449; 1931; 1932; 1936). F_3F_4: 2 males (L-1934; 1935); 3 females (L-1442; 1933; 1938). 14- Camino a Farellones (Lat. 33° 20' S, long 71° 21' W, altitude 1400-1500m): 1980: St_3F_4: 3 males (L-166; 259; 262); 2 females (L- 215; 228a). P_3F_4: 7 males (L-176; 216; 220; 228b; 235; 237; 238); 3 females (L-214; 233; 239). F_3F_4: 3 males (L-175; 217; 234); 1 female (L-174). 15- 1991: St_3F_4: 3 males (L-1669; 1918; 1919); 2 females (L-1691; 1920). P_3F_4: 8 males (L-1670; 1678; 1679; 1916; 1917; 1923-1925); 6 females (L-1672; 1673; 1675; 1677; 1921; 1922). F_3F_4: 2 males (L-1681; 1690); 3 females (L-1422; 1671; 1676). 16- Yerba Loca (33° 19' S, 70° 20' W, altitude 1800 m). 1990: St_3F_4: 2 males (L-1663; 1668); 1 female (L-1682). P_3F_4: 3 males (L-1684; 1685; 1686); 3 females (L-1428; 1438; 1662). F_3F_4: 3 males (L-1425; 1435; 1683); 2 females (L-1660; 1661). 17- El Manzano (33° 35'S, 70° 24' W, altitude 1350-1500 m). St_3F_4: 1 female (L- 1448). P_3F_4: 4 males (L-1047; 1718-1720); 2 females (L-1049; 1724). F_3F_4: 2 males (L-1721; 1722); 1 female (L-1723). 18- Lagunillas (33° 37' S, 70° 20' W, altitude 1500 m). P_3F_4: 4 males (L-1053-1056); 1 female (L-857). F_3F_4: 2 males (L-856; 930). 19- San Alfonso

(33° 43' S, 70° 18' W, altitude 1100-1200 m). St3F4: 3 males (L-199; 208; 377). P_3F_4: 6 males (101; 112; 210; 211; 376; 378); 5 females (L-100; 104; 114; 209; 288). F3F4: 2 males (198; 201); 1 female (L-292). 20- San Gabriel (33° 46' S, 70° 14' W, altitude 1250 m). St_3F_4: 3 males (L-251; 297; 547); 2 females (L-301; 542). P_3F_4: 13 males (L244; 248; 252; 299; 300; 549-551; 553-555; 562; 565); 4 females (L-309; 543; 546; 548). F_3F_4: 9 males (L-245; 246; 249; 252; 290; 540; 541; 545; 656). 21- Yeso Norte (33° 47' S, 70° 12' W, altitude 1320 m). St_3F_4: 1 male (L-1012). P_3F_4: 6 males (L-958; 959; 1013; 1015; 1644; 1645). F_3F_4: 3 males (L-1011; 1014; 1030). 22- Yeso Sur (33° 47' S, 70° 13' W, altitude 1300 m), several years: St3St4: 10 males (L-845; 846; 889-891; 926; 927; 1655; 1739; 1741); 5 females (L-833; 847; 929; 1029; 1037). St_3F_4: 3 females (L-617; 956; 957). St_3P_4: 3 males (L-1035; 1039; 1044); 3 females (L-1009; 1740; 1746). P3St4: 1 male (L-1744). P_3P_4: 2 males (L-1010; 1036); 4 females (L-925; 932; 1042; 1646). P_3F_4: 3 males (L-953; 954; 1043); 3 females (L-888; 1040; 1742). F_3P_4: 1 male (L-1648). F_3F_4: 2 males (L-844; 955); 1 female (L-1038).

II.- The "southern 2n = 34" chromosomal race from:

(A) The Coastal mountain range: 23- Cantillana (33° 55' S, 70° 57' W, altitude 1300-1550 m).1988: St_3 St_4 St_5 St_7: 14 males (L-1085; 1986; 1088; 1089; 1102; 1102a; 1103; 1122; 1125; 1126; 1133-1136); 5 females (L-771; 1087; 1090; 1124; 1127). St_3 St_4 $AF_{5/7}$ $AF_{7/5}$: male (L-1123). 1990: St_3 St_4 St_5 St_7: 21 males. (L-1322; 1323; 1326-1328; 1331-1333; 1335; 1336; 1341; 1504-1506; 1509-1511; 1516-1518; 1529) 15 females (L-1309- 1318; 1507; 1514; 1530; 1532; 1533). St_3 St_4 $AF_{5/7}$ $AF_{7/5}$ 2 males (L-1329; 1515; 1528).

(B) The Andean mountain range from: 25- Los Queñes (35° 07'S, 70° 58'W, altitude 1450 m). St_3 St_4: 26 males (L- 1065; 1066; 1228-1233; 1236; 1237; 1459-1461; 1464-1466; 1469; 1470; 2638; 2640-2646); 13 Females (L-1064; 1067; 1226; 1227; 1235; 1462; 1463; 1467; 1468; 2635-2637; 2639). 26- Volcán Sur (33° 48' S, 70° 09'W, altitude 1415 m). St_3St_4: 8 males (L-604; 605; 678-680; 687-689); 6 females (L- 602; 603; 606; 677; 690; 691).

III.-The "multiple fission 2n = 42-44" chromosome race from:

27- Mina Hierro Viejo (32° 17' S, 71° 00'W, altitude 350 m). With ifferent cytotypes: 20 males (L-1354; 1358-1361; 1608; 1609; 1616-1618; 1807-1812; 1815-1818); 9 females (L-1356; 1357; 1362; 1610; 1612; 1614; 1619; 1620; 1814).

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