Origin of Fueguian-Patagonians: An Approach to Population History and Structure Using R Matrix and Matrix Permutation Methods

ROLANDO GONZÁLEZ JOSÉ,1 CLARA GARCÍA-MORO,1 SILVIA DAHINTEN,2 AND MIQUEL HERNÁNDEZ1
1Universitat de Barcelona, Facultat de Biologia, Unitat d’Antropologia, Barcelona, Spain
2Centro Nacional Patagónico (CONICET), Bvd. Brown s/n. (9120), Puerto Madryn, Argentina

ABSTRACT A complicated history of isolation between Fueguian and Patagonian groups (originated by the appearance of the Straits of Magellan) as much as differences in population structure and life strategies constitute important factors in the clustering pattern of those groups. The aim of this work was to test several hypotheses about population structure and history of Fueguian-Patagonians to propose a model that incorporates predictions for future studies. R matrix methods and matrix permutation analyses were performed upon a data matrix of craniofacial measurements of 441 skulls divided into nine samples pertaining to six Patagonian and three Fueguian populations. Association of biological distances with three matrices representing several settlement patterns was tested using matrix permutation tests. Results of R matrix study show that the minimum genetic distance obtained confirms separation between Fueguians and Patagonians. Moreover, an analysis of residual variances from the expected regression line confirms admixture between Andean and Pampean populations and Araucanian groups, consistent with ethnohistorical observations. A model representing a long history of isolation between Fueguian and Patagonians, rather than a model emphasizing differences in life-strategies, presented the best correlation with the biological distance matrix. Because similar results were already obtained in archaeological, molecular, and morphological studies, a model for the settlement of Tierra del Fuego is proposed. It is summarized by four main hypotheses that can be tested independently by different disciplines in the future. Am. J. Hum. Biol. 14:308–320, 2002. © 2002 Wiley-Liss, Inc.

Two main life strategies evolved in Tierra del Fuego-Patagonia. On one hand, a terrestrial hunting-gathering economy developed among the groups that inhabited the steppe grasslands extending from central Argentina to Patagonia and Isla Grande de Tierra del Fuego. Neither agricultural subsistence nor pastoralism developed south of 32°S latitude (Mena, 1997). The terrestrial people encompassed the Puelches or Pampas, the Tehuelches, and the Selk’nam. The Pampas or Puelches inhabited the pampas north of the Colorado River in central Argentina (Fig. 1). The Tehuelches occupied continental Patagonia; their territory was limited to the north by the Colorado River and to the south by the Straits of Magellan (Fig. 1). Obviously, the same population did not uniformly occupy this vast territory; river basins probably had an important role in biological and cultural differences among the groups (Casamiquela, 1990). Finally, the Selk’nam were confined to the steppe regions from Isla Grande Tierra del Fuego (Fig. 1). Guanaco (Lama guanicoe), one of the four South-American camelids, was the most important prey and the base of their economy.

On the other hand, a marine adaptation mainly based on hunting of sea lions and gathering of bivalves was done in the coastal areas over the Beagle Channel and the Pacific end of the Straits of Magellan. Two Fueguian groups developed this marine hunting-gathering strategy: the Alakuluf and the Yahgan. The Alakuluf occupied the islands and channels of the Chilean Pacific coast, from the Brecknock Peninsula to the Gulf of Penas (Fig. 1). The Yahgan inhabited the coastal areas around the Beagle channel, south to the Brecknock Peninsula, including Cape Horn (Fig. 1). They were the only human group

*Correspondence to: Rolando González José, Universitat de Barcelona, Facultat de Biologia, Unitat d’Antropologia, Av. Ingüida Diagonal 645, 08028 Barcelona, Spain.
E-mail: rgonzale@porihos.bio.ub.es
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ever to have inhabited a region below 55°S latitude (Hernández et al., 1997). Thus, historical groups can be clustered on the basis of one of two possible economic strategies.

The main events of Tierra del Fuego-Patagonia’s settlement are strongly marked by the glacial history in general, and by the presence of land bridges in the Straits of Magellan caused by descent of the sea level. Fluctuations of the Patagonian ice fields in response to climatic change can be identified from the sequences of sediments, the geomorphology of the landscape, and from changes in vegetation patterns in response to climatic change (McCulloch et al., 1997). Recent research demonstrates that crossing from the continental mainland onto Isla Grande de Tierra del Fuego via the connecting land bridge was possible at different times during a broad period spanning the late Pleistocene to early Holocene transition, 14,000 to 8,000 BP (before present) (Borrero and McEwan, 1997; McCulloch et al., 1997). Archaeological evidence seems to indicate that humans were present in Isla Grande, the southern tip of the Americas, between 11,800 and 10,200 BP (Borrero and McEwan, 1997). With the disappearance of the last land bridges of the Straits of Magellan, they probably remained isolated from about 8,000 BP until European contact (Borrero and McEwan, 1997; McCulloch et al., 1997).
Studies based on mitochondria DNA (Lalueza, 1995; Lalueza et al., 1997a) and cranial morphology (González José et al., 2001a,b; Lahr, 1995) are congruent with the idea that, on a continental scale, Fueguian-Patagonian samples tend to cluster in a single group, probably reflecting the coalescence in a common ancestor who settled this region. However, when the comparative framework is refined and geographically constrained, some degree of variability and divergence is observed, either in molecular or morphological traits (Cocilovo and Guichón, 1986; González José et al., 2001; Guichón et al., 1990; Lalueza, 1995; Lalueza et al., 1996, 1997a). Most analyses tend to cluster the three Fueguian groups (Selk’nam, Alalkaluf, and Yahgan) together and to place the nearest continental group (Tehuelche) in an external branch. This pattern is based on several microevolutionary mechanisms. First, the differentiation can be produced by the adaptation of Fueguian groups to the cold and harsh environment of the island. This possibility was explored in several works based on Howells’ craniometric variables (Hernández et al., 1997; Lalueza et al., 1997b). The data indicate evidence of adaptation to a cold environment, particularly in nasal height. The analysis did not include Tehuelche samples, so there was no direct evidence of how adaptation to the cold environment played a role in the differentiation pattern. Other morphological particularities of Fueguian skulls, such as craniofacial robustness and variables of craniofacial width can be attributed to considerable masticatory stress (Hernández et al., 1997). However, this robustness pattern is also observed in Patagonian crania (González José et al., 1999, 2001b; Lahr, 1995). It can be argued that the implementation of different life strategies could account for divergences in cranial morphology, either as an adaptive response to the alimentary behavior, or as a product of a differential long-distance migration of maritime populations down the Pacific archipelago (Borrero, 1997). In this context, some have proposed a model in which the settlement of Tierra del Fuego was done by two different routes, one along the Pacific border, giving place to the marine hunter-gatherers, and the other by the Atlantic coast, constituted by terrestrial hunting-gathering groups (Chapman, 1982; Guichón et al., 1990).

<table>
<thead>
<tr>
<th>TABLE 1. List of craniometric variables</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maximum frontal breadth</td>
</tr>
<tr>
<td>Bzygomatic breadth$^1$</td>
</tr>
<tr>
<td>Nasion-protonion height</td>
</tr>
<tr>
<td>Nasal height$^1$</td>
</tr>
<tr>
<td>Orbit height left$^1$</td>
</tr>
<tr>
<td>Nasal breadth$^1$</td>
</tr>
</tbody>
</table>

$^1$Howells (1973).
$^2$Martin and Saller (1957).

Another factor influencing the pattern of differentiation could be geographic isolation related to the rising of the sea level around 8,000 years BP. This gave rise to the Straits of Magellan and the consequent isolation of the Fueguian with respect to the continental groups, the latter were exposed to gene flow with other Amerindian populations. As an example, it is known that the central Argentina and central Andean zones suffered an invasion by the Araucans from central Chile around 1,000 BP (Mena, 1997). South of the Straits of Magellan, gene flow was presumably restricted to intra-Fueguian interchanges, with little influence of “external” sources at least for the Selk’nams and Yahgan. Lanata (2000) also suggests that in Isla Grande, the Andes functioned as a geographical barrier separating the Selk’nam group from the southern marine hunter-gatherers. Obviously, any combination of these factors could be also suggested.

Recent advances on the genetics of quantitative traits and numerical testing of hypotheses can be useful to evaluate these issues. These techniques were already used to study migration, gene flow, and settlement patterns of classical quantitative traits such as anthropometries (Relethford, 1991; Relethford and Blanegro, 1990; Williams-Blanegro and Blangero, 1989) and craniometries (González José et al., 2001b; Konigsberg and Blangero, 1993; Konigsberg and Öusley, 1995; Powell and Neves, 1999; Relethford, 1994; Relethford and Harpending, 1994).

The objective of this work was to consider the biological variation as reflected in cranial morphology with analyses based on quantitative genetics, and to test the statistical fit of the observed variability with hypotheses about the origin of divergence among Fueguian-Patagonian populations.
MATERIALS AND METHODS

Thirteen metric variables (Table 1) were measured on 441 skulls belonging to nine populations assigned to the historical groups described above. Martin and Saller (1957) and Howells (1973) originally described the variables used. The variables reflected mainly facial morphology to avoid the influence of artificial cranial deformation, which is present in some Tehuelche crania. Four samples can be attributed to the Tehuelche group, but since they inhabited different river basins the groups were designated following a geographical criterion. Thus, samples were Pampas, Río Colorado Tehuelches, Río Negro Tehuelches, Río Chubut Tehuelches, pre-Andean Tehuelches, and Golfo San Jorge Tehuelches, Selk’nam, Alakaluf, and Yahgan. Geographic locations is shown in Fig. 1, and sample sizes are listed in Table 2. Characteristics of the Fueguian skull collections were already described by Hernández et al. (1997). Samples were obtained from the collections belonging to the Museo de la Plata (La Plata, Argentina), Museo Etnográfico J.B. Ambrosseti (Buenos Aires, Argentina), Centro Nacional Patagónico (CONICET, Puerto Madryn, Argentina), and the Musée de l’Homme (Paris, France). Skulls were sexed according to Buikstra and Ubelaker (1994).

The traits were corrected for sex-related size differences using z-score standardization within each sex (Relethford, 1994; Williams-Blangero and Blangero, 1989). Biological distances were assessed using Mahalanobis generalized distances ($D^2$) after modifications of Williams-Blangero and Blangero (1989). These modifications assume an additive polygenic model for the traits in which the expectation of environmental deviations is zero. The phenotypic variance, composed of genetic and environmental components ($\sigma^2_p = \sigma^2_g + \sigma^2_e$) must be greater than, or equal to the genetic variance ($\sigma^2_p \geq \sigma^2_g$). These authors demonstrated that “$D^2$ represents a matrix containing the minimum genetic distances derived from the phenetic variation” (Williams-Blangero and Blangero, 1989, p 5). The resulting equation can be written as:

$$d^2_{ij} = r_{ii} + r_{jj} - 2r_{ij}$$

in which $r_{ij}$ are the elements of an R matrix computed for each trait in populations i and j (Relethford et al., 1997).

Detection of differential gene flow was estimated following the model proposed by Harpending and Ward (1982) and extended to quantitative traits by Relethford and Blangero (1990). This model states that, under certain assumptions, observed and expected genetic or phenotypic variances can be compared to assess the effects of differential external gene flow (Relethford and Blangero, 1990). After this extension, and under certain conditions, it can be asserted that greater than average gene flow from an external source will result in a population having greater within-group phenotypic variance than expected. Conversely, less than average gene flow from an external source will result in a population having less within-group phenotypic variance than expected. Estimations of distance to the centroid ($r_{ii}$), observed and expected within-group phenotypic variance, Fst values, and distance between groups, were obtained after an R matrix based on the Howells (1973) and Martin and Saller (1957) variables. Analysis of data and computation of parameters were performed using the software RMeta for Windows v. 4.0 provided by
Dr. J. Relethford at the World Wide Web (http://konig.la.utk.edu/relethsoft.html).

To test the fit of several hypotheses about the differentiation of populations, a series of matrix permutation test was developed.

In a typical matrix permutation study, dissimilarities between the samples are estimated after any character observable in the population and are then expressed in a distance or dissimilarity matrix. For that, hypothetical differences expected under a particular model are used to construct a design matrix (Waddle et al., 1998). A design matrix describes the relative distances among populations expected under a particular model (Waddle et al., 1998). The actual values assigned to the distances in a design matrix are chosen by the investigator and depend on the model (Waddle et al., 1998). Matrix permutation studies and construction of design matrices are well described in several works by Livshits et al. (1991), Sokal et al. (1992, 1997), Waddle (1994), and Waddle et al. (1998). An appropriate design matrix is critical to successful interpretation of an observed distance matrix (Sokal et al., 1997).

Mantel tests (Mantel, 1967) were used to estimate the level of correlation between the observed and the design matrices. In addition, Smouse-Long-Sokal tests (Smouse et al., 1986) were used to yield partial matrix correlations. The Smouse-Long-Sokal method extends Mantel's statistic to three or more matrices and tests whether an association between matrix A and B is significant when one or more matrices C, D, ... are held constant. Smouse-Long-Sokal test was used to test partial correlations after removing the effects of geography as well as those of competing models. Mantel and Smouse-Long-Sokal tests were computed using the program NTSYSpc, version 2.10d (routine mxcomp). P values reported here were obtained after 100,000 permutations out of 362,880 (99) total possible permutations.

To evaluate competing hypotheses about Tierra del Fuego-Patagonia's settlement, three design matrices were described and are summarized in Table 3.

**Design 1**

The evolution of terrestrial and marine life-strategies lead to changes in craniofacial morphology and is the main factor responsible for the divergences among Fueguian-Patagonian populations. In consequence, the distances between pairs of terrestrial hunter-gatherers will always be lower than those between terrestrial and marine hunter-gatherers and vice versa. An arbitrary distance of 0 was assigned to the comparisons among groups sharing the same life strategies and a distance of 1 to the opposite case.

**Design 2**

Tests the hypothesis that geographic isolation due to the emergence of the Straits of Magellan makes affinities closest among Fueguian populations. Then, affinities are lower between Fueguian populations (they

<table>
<thead>
<tr>
<th>Distance between</th>
<th>Design 1</th>
<th>Design 2</th>
<th>Design 3</th>
<th>G</th>
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</thead>
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<td>0</td>
<td>0</td>
<td>334.1</td>
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<td>0</td>
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<td>PAM-TPA</td>
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<td>0</td>
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<td>ALA-SEL</td>
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<tr>
<td>SEL-YAH</td>
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<td>0</td>
<td>0</td>
<td>195.0</td>
</tr>
</tbody>
</table>

See the text for design's definitions. PAM, Pampas; TRC, Rio Colorado Tehuelches; TRN, Rio Negro Tehuelches; TCH, Rio Chubut Tehuelches; TPA, pre-Andean Tehuelches; TJSJ, Gulf San Jorge Tehuelches; ALA, Alakaluf; SEL, Selk'nam; YAH, Yahgan.
are separated with a distance of 0), which share both ancestry and geographic isolation. Conversely, comparisons between Fueguian and Patagonian populations, which share only ancestry (but not geography), are assigned a distance of 1.

Design 3

This is similar to design 2, except that Alakaluf populations play a role as a “bridge” between Patagonia and Tierra del Fuego via the southern part of the Andes. This possibility is suggested by some archaeological observations (Mena, 1987) and by the fact that wide distribution of the Alakaluf may have allowed some degree of gene flow with continental groups. The design matrix is equal to that constructed in design 2, except for comparisons involving the Alakaluf, which were assigned a value of 0.5.

In addition to the three design matrices, a geographic distance matrix was constructed in which elements were the great circle distances in kilometers between the populations (Table 3).

RESULTS

Results are presented first for the $R$ matrix analyses, which provide a general overview of variability within and between groups, and thus for matrix correlation methods.

The minimum $Fst$ was equal to 0.096. The minimum $Fst$ is obtained considering that all heritabilities are equal to 1 and assuming that the additive genetic covariance matrix is proportional to the phenotypic covariance matrix (Williams-Blangero and Blangero, 1989). This is a conservative statistic because it implies that the minimum $Fst$ should be less than an estimate of $Fst$ computed from genetic markers (Relethford, 1994).

To characterize Fueguian-Patagonian variability, parameters derived from the Relethford and Blangero (1990) methodology were estimated. The values of distance from the centroid and observed/expected within group phenotypic variance are presented in Table 2. These values can be compared to assess the effects of differential external gene flow (Relethford and Blangero, 1990). The plot of observed mean phenotypic (genetic) variance versus genetic distance from the centroid for the Fueguian-Patagonian populations is shown in Figure 2. The line indicates the expected regression line derived from the multivariate extension of the Harpending and Ward (1982) model (Re-
TABLE 4. Matrix of unbiased minimum genetic distances (B) computed according Williams Biangero and Blangero (1989), and Relethford and Blangero (1990)

<table>
<thead>
<tr>
<th></th>
<th>PAM</th>
<th>TRC</th>
<th>TRN</th>
<th>TCH</th>
<th>TPA</th>
<th>TSJ</th>
<th>ALA</th>
<th>SEL</th>
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<tr>
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<td>TPA</td>
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<td>0.293</td>
<td>0.386</td>
<td>0.217</td>
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<tr>
<td>YAH</td>
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<td>0.320</td>
<td>0.261</td>
<td>0.182</td>
<td>0.262</td>
<td>0.198</td>
<td>0.284</td>
<td>0.079</td>
</tr>
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</table>

PAM, Pampas; TRC, Río Colorado Tehuelches; TRN, Río Negro Tehuelches; TCH, Río Chubut Tehuelches; TPA, pre-Andean Tehuelches; TSJ, Golfo San Jorge Tehuelches; ALA, Alakaluf; SEL, Selk'nam; YAH, Yahgan.

Fig. 3. Plot of the first two scaled eigenvectors obtained after Principal Coordinates Analysis using R matrix data. The first and second eigenvalue accounts for 57.8% and 16.3% (total, 74.1%) of the variation respectively. PAM, Pampas; TRC, Río Colorado Tehuelches; TRN, Río Negro Tehuelches; TCH, Río Chubut Tehuelches; TPA, pre-Andean Tehuelches; TSJ, Golfo San Jorge Tehuelches; ALA, Alakaluf; SEL, Selk’nam; YAH, Yahgan.

...than average admixture. The Fueguian group seems to show average admixture, whereas the position of the Tehuelches and Pampas suggest slightly less than average admixture.

The minimum genetic distances matrix obtained after the Relethford and Blangero (1990) method (B) is presented in Table 4. The plot of the two first eigenvectors obtained after computing the Principal Coordinates Analysis using the R matrix are shown in Figure 3. Fueguian samples clearly form a single cluster with low distance values between them and clearly separated from the continental group. Furthermore, the pre-Andean Tehuelches (TPA) depart from the remaining groups.

Permutation matrix methods were performed upon five matrices: B, a matrix of unbiased distances among groups considering equal population sizes; D1, D2, and D3, three design matrices representing several hypotheses about the origin of divergences between groups; and G, a matrix reflecting geographic separation.

Results of the Mantel tests are presented in Table 5. D1 and D2 as well as D1 and D3 are not intercorrelated. This indicates that except for designs 2 and 3, the models are...
ORIGIN OF THE FUEGUIAN-PATAGONIANS

TABLE 5. Matrix correlations between minimum genetic distances (B) three designs (D1-D3), and a matrix of spatial separation (G).

<table>
<thead>
<tr>
<th></th>
<th>r</th>
<th>P Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>BxG</td>
<td>0.620</td>
<td>0.007</td>
</tr>
<tr>
<td>BxD1</td>
<td>0.394</td>
<td>0.056</td>
</tr>
<tr>
<td>BxD2</td>
<td>0.880</td>
<td>0.012</td>
</tr>
<tr>
<td>BxD3</td>
<td>0.708</td>
<td>0.012</td>
</tr>
<tr>
<td>GxG</td>
<td>0.338</td>
<td>0.055</td>
</tr>
<tr>
<td>GxD2</td>
<td>0.724</td>
<td>0.012</td>
</tr>
<tr>
<td>GxD3</td>
<td>0.852</td>
<td>0.004</td>
</tr>
<tr>
<td>D1xG</td>
<td>0.570</td>
<td>0.005</td>
</tr>
<tr>
<td>D1xD2</td>
<td>0.427</td>
<td>0.0057</td>
</tr>
<tr>
<td>D1xD3</td>
<td>0.889</td>
<td>0.004</td>
</tr>
</tbody>
</table>

See text for description of matrices and tests.

TABLE 6. Partial Mantel correlations among one measure of biological distance (B) and three design matrices (D1-D3) with spatial separation (G) held constant.

<table>
<thead>
<tr>
<th></th>
<th>r</th>
<th>P Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>BxD1</td>
<td>0.249</td>
<td>0.0491</td>
</tr>
<tr>
<td>BxD2</td>
<td>0.796</td>
<td>0.0002</td>
</tr>
<tr>
<td>BxD3</td>
<td>0.436</td>
<td>0.0060</td>
</tr>
</tbody>
</table>

self-explanatory and represent independent, antagonistic approaches. This is an expected result, because only values involving ALA are variant between the two models. B, D2, and D3 were correlated with geographic separation estimated as linear distances in kilometers (G). Additionally, B was correlated with D2 and D3. The highest correlation value was observed in the comparison B-D2 (r = 0.88, P = 0.0117).

Because both biological variation and two of the designs were closely related with geographic distances, results of correlations could be best interpreted as partial matrix correlations holding geography constant (Sokal et al., 1992; Waddle et al., 1998). The partial Mantel correlations among B and the three design matrices with spatial separation held constant are shown in Table 6. When the effects of spatial separation are removed, the models considering strong influence of isolation due to the Straits of Magellan (D2 and D3) seem to be the most solid explanation of the pattern of craniometric variability among Fueguian-Patagonians. Using a conservative P value for the Smouse-Long-Sokal method, e.g., P = 0.001, it can be reasonably certain that the partial correlation coefficients are significant at P < 0.05 (Oden and Sokal, 1992).

Because the Smouse-Long-Sokal test can be extended to control the effects of more than one matrix, one additional analysis was done to further corroborate the significance of B-D2 and B-D3 correlation as described in Sokal et al. (1992). This approach consists of partial correlations of B on D2 (and B on D3) holding geographic separation as much as the remaining models constant until all matrices are considered. The results (Table 7) confirm the performance of D2. Note, that the correlation of B on D2 with added distance matrices held constant do not decrease further and continue to be significant. Conversely, the association B-D3 diminishes when the remaining matrices are held constant.

DISCUSSION

Before evaluating the Fueguian-Patagonian populations in a local context, it must be noted that their position in the settlement of the America’s is unresolved, or at least, controversial. Lahr (1995) suggested that both Fueguian-Patagonian and Paleoamerican populations might reflect the morphology of a more generalized Mongoloid ancestral group. In agreement with this idea, Lalueza et al. (1997a), in a study of mtDNA in Fueguian groups, show that the exclusive presence of lineages C and D at the southern extreme of the continent traces back to a population of more ancient ancestry, distinct from the Amerindian populations harboring all four primary lineages. In previous studies, it was demonstrated that Fueguian-Patagonian samples could be of importance when discussing settlement models for the America’s mainly because their morphology seems to depart from the classical Amerindian pattern of epigenetic (González José et al., 2001a) and craniometric (González José et al., 2001b) variation. Furthermore, matrix permutation analyses were unable to clearly discriminate between models in which the relative position of Tierra del Fuego-Patagonia sample with respect to Paleoamerican samples was arbitrarily altered (González José et al., 2001b). Discussion of parameters and models in a more regional context might shed some light on this issue.

The Fst value obtained here (0.096) is a foreseeable result. As stated above, when complete heritability is assumed, Fst becomes a conservative statistic: minimum
Fst value should be less than estimates of Fst computed from genetic markers (Relethford, 1994). As expected, the Fueguian-Patagonian Fst value is lower than estimations of Barbujani et al. (1997) based on worldwide DNA diversity (Fst = 0.156).

A striking result is observed in Figure 2, where Tehuelches from Andean zones show more variability than expected. The position of Fueguians suggests average admixture, and the position of the remaining Tehuelche groups suggest less than average to average admixture. In this regard, and as stated by Relethford and Harpending (1994), within-group variation, whether assessed through conventional genetic markers, mtDNA or morphological traits, should reflect several parameters and is a function of population size, migration rates (both local and long-range), gene flow, genetic drift, mutation rate, etc. (Relethford and Harpending, 1994). In general terms, one can classify those factors as changes in population structure or in population history (Templeton et al., 1995). Population structure is considered as the apportionment of genetic variation among interbreeding demes due to processes such as gene flow and genetic drift. Conversely, population history refers to genetic changes attributable to non-recurrent historic events such as range expansion, range contraction, and population replacement (Powell and Neves, 1999; Templeton et al., 1995). In the case of Fueguian-Patagonian populations, some precise considerations about the origin of within and between group variance patterns can be established considering their population structure and history.

First, differences in population size have some effect on genetic variability of these groups. Because direct estimations of population size are not available (except for Selk’nam (Garcia-Moro, 1992; Garcia-Moro et al., 1997)), the R matrix approach was used to simulate a hypothetical demographic scenario in which departures from the expected regression line are minimized.

In the present case, experiments were done by changing population sizes, but the distance matrix obtained was unable to correlate significantly with the design matrices. The development of better populations size estimates will probably improve the results obtained with these methods.

Second, historical events of interest can be explored. Fueguian populations were geographically isolated during the last 8,000 years and would be expected to show high rates of local migration. Furthermore, admixture with continental groups was almost impossible, at least for the Selk’nam and Yahgan. Closeness among Fueguians observed in the dispersion plot (Fig. 3) as much as their, position with regard to the expected regression line (Fig. 2) could be caused mainly by such isolation. This observation is congruent with ethnological studies, which documented interethnic contacts among Fueguians (Gusinde, 1979, 1989; Martinic, 1999).

The pattern of dispersion around the regression line is strongly determined by the outlier character of the Pre-Andean Tehuelches, which shows more than average admixture. Under the Relethford and Blangero (1990) model, positive residuals for a population may reflect: (a) higher levels of long range gene flow from an “outside” source resulting in greater heterozygosity; (b) a higher mutation rate than other groups considered (Powell and Neves, 1999); (c) a larger, effective population size or differential timing of population growth than other populations (Powell and Neves, 1999; Relethford, 1995); or (d) nonrandom sampling effects or population pooling that artificially inflate within-group variance (Powell and Neves, 1999). In the present case study, it is suggested that the most parsimonious way to interpret the greater amount of variation observed among pre-Andean Tehuelche is to assume that this population experienced high levels of gene flow with the Araucanian elements inhabiting or entering from Central Chile. It is very difficult to accept that the entire deviation from the expected line is
due to a greater population size of pre-Andean Tehuelche.

Model 2 (D2) and Model 3 (D3) represent a history of both, isolation between Tehuelche and Fueguian and Fuegian admixture forced by shared isolation. Note that D2 and D3 were the unique models showing positive, highly significant correlation with the minimum genetic distance matrix (B). Holding constant the remaining matrices did not result in a weakening of association between B and D2/D3, but maintained similar levels of correlation. The analysis was unable to discriminate between the effects of D2 and D3. Probably, the role of Alakaluf populations as a contact between continental and insular genetic pools in the last 8,000 years may be demonstrated in the future with a more accurate assessment of demographic relationships.

Hernández et al. (1997) suggested that Fueguian nasal morphology could be an adaptive response to the harsh cold climate. Since the pattern of differentiation remains equal when nasal variables are removed (results not shown), and climate is also harsh and cold in continental Patagonia (Gómez Otero et al., 1998), it is postulated that Tehuelche also experienced some degree of adaptation in their nasal morphology to cold climates that could be parallel to that of Fueguians.

To delineate the settlement of a region, several characters and approaches to the problem must be considered. If it is assumed that 1) Fueguian-Patagonians shared a common ancestor, 2) Tierra del Fuego was first settled around 10,000 to 12,000 years BP by groups of undifferentiated economy, 3) Fueguian populations remained isolated from the continent during the last 8,000 years and were less numerous than the continental populations, and 4) Fueguian groups maintained some degree of gene flow between them, then several predictions about the behavior of biological and genetic parameters can be suggested. These four points can be handled as independent working hypotheses, but, when considered together, they can be viewed as a settlement model. Analyzing the present results and evidence from other sources, there is some support for the proposed model.

Data supporting the first point (common ancestry) was discussed in several papers (Cocilovo and Guichón, 1986; González José et al., 2001, 2001b; Lahr, 1995; Lalueza et al., 1996, 1997a). There is concurrence about the clustering pattern of Fueguian-Patagoniansns compared with other world populations.

With respect to the second point, archaeologists mainly focused on the origins of the divergence between marine and terrestrial adaptations (Borrero, 1990, 1997; Chapman, 1987; Legoupil and Fontugne, 1997; Menghin, 1952; Orquera et al., 1987; Piana, 1984). If marine and terrestrial economies were well differentiated prior to the first settlement of Tierra del Fuego, then early coastal archaeological sites should show specialized marine remains (with the opposite for continental sites). Nevertheless, after an extensive examination of the archaeological remains from sites on the Beagle Channel (Lancha Packewaia and Tunel), Piana (1984) and Orquera et al. (1987) concluded that marine adaptation was developed once the populations were inside Isla Grande from Tierra del Fuego (note that canoeing was impossible until the wood biome extended into the Fueguian channels at 8,000 years BP). Moreover, Legoupil and Fontugne (1997) observed that the more ancient archeological sites in Tierra del Fuego are located in transitional maritime/terrestrial zones, evidencing a lack of specificity in habitat exploitation. Thus, archaeological data suggest a cline from strongly maritime cultures in the islands and channels to the west and the far south, to strongly terrestrial cultures in the steppes in the east and far north (Borrero, 1997). Support for this point is suggested in low correlation between D1 and B (Table 6), i.e., life-strategy was clearly not associated with craniofacial morphology.

The third and fourth points of the model can be better viewed from a biological perspective. After analyzing mtDNA variation, Lalueza et al. (1997a) found a lack of founding Amerindian mitochondrial DNA lineages in aborigines from Tierra del Fuego-Patagonia. Lalueza et al. (1997a) concluded that genetic isolation would have contributed to prevent haplogroups A and B from entering the genetic pool of ancient Fueguian-Patagoniansns populations. According to these results, the analysis of craniofacial morphology suggested that Fueguian populations show high closeness, probably due to a combination of isolation
from an “outside” source of variability, low population sizes over several generations, and high rates of gene flow among them.

Discussion and future evaluation of this model must include additional groups of interest (e.g., southern Tehuelche or Aonikenk and northern Alakaluf or “Chonos”). Nevertheless, some predictions can be made about the behavior of several characteristics and methodologies to test aspects of the model. For example, if point three isolation and smaller population size reflects appropriately the settlement of Tierra del Fuego, then spatial autocorrelation analysis (Sokal and Oden, 1978a, 1978b; Sokal and Thomson, 1998; Sokal et al., 1986) applied on high mutation rates systems should show a monotonic clinal pattern for continental populations and a disruption of that pattern when Fueguian groups are included. Spatial autocorrelation analysis can also be of great use to test the clinal transition of splachnocranial measurements proposed by Cocilovo and Guichón (1986). Extension of spatial autocorrelation tests to archaeological data may be of interest to test the validity of a clear-cut limit between economies and to compare autocorrelation curves obtained from other sources.

Geographic isolation can be tested in several traits. Because gene flow is commonly restricted by geographical distance (Wright, 1943), the present model is not expected to yield a strong positive relationship between geographical distance and genetic distance (Templeton, 1999). Since the model reflects a single origin and a scenario in which all Fueguian populations “split” from continental populations at the same time, then all genetic distances between Fueguian and non-Fueguian populations must have the same expected value (Templeton, 1999). However, in the case of craniofacial morphology, geographic separation was moderately correlated with biological distances (Table 5). When geographic variation is tested for significant departures from randomness, the effects of coding the data should be noted (Sokal, 1979). The choice of a given geographic distance model depends on the nature of the mechanisms involved in the origin of geographic variation. Thus, inspection of different patterns of spatial separation should be considered in future studies to evaluate the predictions. Other parameters such as Fst and within-group genetic variance can be obtained from molecular data to test congruence with the present findings. Additionally, estimates of effective population sizes can be obtained independently using molecular traits. In fact, under selective neutrality and mutation-drift equilibrium, it might be expected that the genetic diversity within a population is related to the size of the population (Hawks et al., 2000). Following this approach, better estimates of relative population sizes, such as the estimates of Selk’nam population size computed by García-Moro et al., (1997) after missionary registers, can be further tested.

Model-bound methods, such as R matrix techniques, make clear assumptions regarding the mode of transmission of underlying genotypic variation expressed in the phenotype, and evolutionary and demographic parameters affecting population structure (Powell and Neves, 1999; Relethford and Lees, 1982). The approach used here provides parameter estimates that are usable in future discussions if the settlement of the southern part of the America’s, and that improve the comparative utility of the craniometric data available for Fueguian-Patagonians.

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LITERATURE CITED


Chapman A. 1982. Drama and power in a hunting so-
ciety: The selknam of Tierra del Fuego. Cambridge: Cambridge University Press.

Chapman A. 1987. La Isla de los Estados en la Pre-

123.

García-Moro C. 1992. Reconstrucción del proceso de extinción de los Selk’nam a través de los libros mis-


González José R, Zavatti J, Dahinten SL. 1999. Di-


Guichón RA, Martí Í, Aspillaga A, Cociloja JA, Roth-

Gusinde M. 1979. Expedición a la Tierra del Fuego. [1919/ 
24]. Santiago de Chile. Editorial Universitaria.

Gusinde M. 1989. Los Índios de Tierra del Fuego. [1937] 
Buenos Aires: Centro Argentino de Etnología Ameri-
cana.


Hernández M, Laluzea C, García-Moro C. 1997. Fue-
guian cranial morphology. The adaptation to a cold, harsh environment. Am J Phys Anthropol 103:103–
17.


Konigsweg LW, Blangero J. 1993. Multivariate quan-
titative genetic simulations in anthropology with an example from the South Pacific. Hum Biol 65:897–
915.

Konigsweg LW, Ousley SD. 1995. Multivariate quan-

Lahr MM. 1995. Patterns of modern human diversifi-

Laluzea C. 1995. Recuperación de DNA mitocondrial y caracterización de variabilidad en poblaciones anti-
guas. Doctoral dissertation, University of Barcelona, Spain.

Laluzea C, Hernández M, García-Moro C. 1996. Cra-
niometric analysis in groups from Tierra del Fuego/

Laluzea C, Pérez-Pérez A, Prats E, Cornudella L, Tur-
bón D. 1997a. Lack of founding amerindian mito-

Laluzea C, Hernández M, García-Moro C. 1997b. La 
morphología facial de las poblaciones fueguinas: z re-

Lamata JL. 2000. The world’s southernmost foragers: The native diversity of Tierra del Fuego (Manuscript).

Legoupil D, Fontugne M. 1997. El poblamiento marit-
time en los archipielagos de Patagonia: Núcleos an-

49:131–146.


McCulloch RD, Clapperton CM, Rabassa J, Currant 
AP. 1997. The natural setting: The glacial and post-
glacial environmental history of Fuego-Patagonia. In: 
McEwan C, Borrero LA, Prieto A, editors. Patagonia; 
Natural history, prehistory and ethnography at the uttermost end of the earth London: British Museum 

Mena F. 1987. Investigaciones sobre cazadores con-
tinentales en Aisën, Chile. Con I Jornadas Arq Pat 

Mena F. 1997. Middle to late Holocene adaptations in 
Patagonia. In: McEwan C, Borrero LA, and Prieto A, 
editors. Patagonia: Natural history, prehistory and 
ethnography at the uttermost end of the Earth. Lon-

Menghin O. 1952. Fundamentos cronológicos de la 
prehistoria de la Patagonia. Runa, 5:23–43.


Evolución adaptativa humana en la región del can-
al Beagle. 1er. Jornadas de Arqueología de la Patagonia. 
Gobierno de la Provincia del Chubut. Se Human 
2:201–209.

Piana EL. 1884. Arrincenamiento or adaptación en 
Tierra del Fuego: Ensayos de Antropología Argentina. 

Powell JP, Neves WA. 1999. Craniofacial morphology of the first Americans: Pattern and process in the pe-

Relethford JH, Lees FC. 1982. The use of quantitative 
traits in the study of human population structure. 

Relethford JH, Blangero J. 1990. Detection of differ-
ential gene flow from patterns of quantitative varia-

Relethford JH. 1991. Genetic drift and anthropometric 