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The Settlement of Patagonia: A Matrix Correlation Study

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Abstract Matrix correlation represents an innovative methodology to evaluate the explanatory power of several hypotheses by measuring their correspondence with observed morphological variation. In this paper, we view the origins of Patagonians from a matrix correlation approach. Personal and published data on nonmetric cranial traits were used to estimate a biological distance matrix involving five major groups from Patagonia and two from the northwest and northeast regions of Argentina. To evaluate correspondence with other important factors, we used a geographic distance matrix and four design matrices, representing several patterns of settlement and differentiation. Biological distance was found to be strongly associated with spatial separation; the correlation between geography and nonmetric cranial distances was highly significant. When geographic distance is held constant, correlation between a model representing high levels of heterogeneity between the samples and morphological (nonmetric) variation becomes highly significant.

In 11,000 BP our species reached the last inhabitable place in the world, Patagonia (Borrero and Franco 1997). From that time until the Europeans would come to occupy this territory, hunting and gathering was the strategy for settlement across arid landscapes (Borrero 1994–95), Fueguian shores (Legoupil and Fontugne 1997), and the Andes (Mena Larraín 1987; Borrero 1994–95).

Discussion of the affinities and adaptation processes of the first Patagonians has generated a considerable number of publications in such disciplines as archaeology (Gusinde 1937; Bird 1946a, 1946b; Cooper 1946a, 1946b, 1946c, 1946d; Emperaire 1963; Mena Larraín 1987; Borrero 1994–95), linguistics (Casamiquela 1990; Viegas Barros 1994), quaternary research (Menghin 1952; Borrero 1994–95; Legoupil and Fontugne 1997), genetics (Lalueza et al. 1997), and morphological studies (Lahr 1995, 1996; Lalueza et al. 1996; Hernández et

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al. 1997; González José et al. 1999). In a more general context, numerous scholars have researched the peopling of Patagonia and Argentina. However, questions about the populations—their biological affinities, their origins, and how they dispersed in Patagonia—remain unresolved and controversial. Salzano and Callegari-Jacques (1988) summarized the main migratory movements in South America, introducing a pathway to Patagonia as a secondary branch of the classical route along the Pacific Coast and the Andes. According to the authors, the routes indicated should be considered preliminary, since they are based in geographical logic and chronological differences. Nevertheless, they can be used as working hypotheses. Studying 13 blood polymorphisms, the same authors found an important role played by geographical proximity in the formation of clusters and distinguished four centers of dispersion or convergence of people, two in the north and two in the central-southern part of the continent. Unfortunately, the authors' analyses do not include Patagonian samples.

Study of the cranial morphology of the first inhabitants of Patagonia has not contributed to the debate, for two principal reasons. Firstly, the native populations are, nowadays, highly interbred or completely extinct. Secondly, skull collections are dispersed over several institutions in Europe and South America, making it difficult to achieve acceptable sample sizes (González José 1998). Nevertheless, some studies can be cited. In a previous work (González José et al. 1999), we investigated the biological affinities of four groups from northern Patagonia. The series pertaining to the same cultural complex exhibited an unexpected morphological divergence, suggesting complicated mechanisms of spreading and contact between groups. In different analyses and series Lahr (1996), Dahinten et al. (1999), and Luis et al. (1999) demonstrated that Patagonians' cranial morphology departs from the typical Mongoloid pattern. Other authors (Mendez and Salceda 1995) studied intergroup relationships on the basis of three skull samples from northwestern, northeastern, and southern Argentina. They suggested a greater mobility of primitive populations from the northeast to the south, with a later modification and an increase in the uniqueness of morphological variation due to the coming of new population waves in northwest present-day Argentina. Lalueza et al. (1996) and Hernández et al. (1997) analyzed large craniometrical samples of Fueguian groups and demonstrated that both marine hunter-gatherer (or canoeros) groups and terrestrial groups tended to form a single cluster, indicating a similar morphological pattern.

The existence of two different migratory routes in the peopling of Tierra del Fuego, one following the Pacific Coast and the other following the Atlantic Coast, was hypothesized by several authors (Rothammer et al. 1984; Cocilovo and Di Rienzo 1984–85; Guichón et al. 1986; Ghichón and Varela 1990). Lahr (1996), in an extensive work, stated that populations from Tierra del Fuego and Patagonia exhibit a very robust morphological pattern and may be seen as having retained, to a higher degree, the morphology of the first inhabitants of the continent. This assessment leads to the logical conclusion that it is not possible to derive all

South American aboriginal populations from a single, morphologically derived ancestral source.

The aim of this study is to test some hypotheses examining nonmetric cranial variation in seven Argentinian populations and to evaluate their association with spatial separation and with several models for the peopling of Patagonia. In biology, observable relationships are frequently expressed as a distance or dissimilarity matrix between all pairs of a set of individuals or samples (Sokal et al. 1997). Thereafter, one can state the hypothesized relationships among pairs of a set of entities as distance matrices, the "design matrices" (Waddle 1994; Sokal et al. 1997). In the first part of our analysis we use matrix correlation methods to test congruence between different measures of biological distance (Mantel 1967; Smouse and Long 1992; Smouse et al. 1986). Next, we quantify the association between measures of biological distance and geographic separation. Finally, we evaluate the consensus between biological variation and hypothesized variation represented in four design matrices (Waddle 1994; Sokal et al. 1992, 1997). Design matrices were constructed to represent specific competing models of Patagonia's settlement.

Materials and Methods

The Sample. In order to carry out the present study, we used data regarding samples and frequencies of nonmetric cranial traits as published by De Stefano and Macchiarelli (1979, 1980), Mendez and Salceda (1995), González José (1998), and González José et al. (1999). Only adult individuals were considered in those studies. Mendez and Salceda, and De Stefano and Macchiarelli used the Berry and Berry (1967) set of traits, whereas González José et al. adopted the Buikstra and Ubelaker (1994) set. We compared the three data sets and selected 20 traits that can be found in all three sources.

Some considerations must be noted regarding the pooling of data from different sources, especially regarding the method in which frequencies were determined. Since many traits are bilateral, frequencies can be obtained in several ways. Here, we followed the methodology proposed by Korey (1980), using the cranium (rather than the side) as the unit of analysis. Fortunately, Mendez and Salceda (1995) followed the same criteria. De Stefano and Macchiarelli (1979, 1980) used sides as the unit, but they provided an extensive table in which detailed information can be obtained for each trait and each side. Following that table we computed frequencies using crania as the unit. In addition, several studies have demonstrated that side differences are practically irrelevant (Cossedu et al. 1979; Buikstra 1973; González José 1998), and that the characters used in this study are not intercorrelated (Berry and Berry 1967; Kellock and Parsons 1970; González José 1998).

Finnegan and Rubison (1980) recommended against pooling data from different observers; nevertheless, Konigsberg (1988) reported low levels of interob-

server error for a similar study. Our experience has been that interobserver variation is important when different definitions of the expression of a given trait are involved. However, the three sources considered here deal with a set of traits (Berry and Berry 1967) that is clearly stated and accepted. This method of handling data permits the study of a sample dispersed throughout the world.

The 253 skulls included in this study were divided into seven subsamples according to geographical location (Figure 1). The northwest sample (NWA, n =32) includes sedentary groups whose subsistence was based on agriculture and who were directly or indirectly influenced by the Andean culture (Méndez and Salceda 1995). People who inhabited the northeast grasslands (NEA, n = 33) had a mixed economy of agriculture, hunting, fishing, and harvesting. The Chubut River Valley (CRV, n = 70), San Jorge Gulf (SJG, n = 38), and Pre-Andean (PRE, n = 20) populations were continental terrestrial hunter-gatherers assembled under the ethnographic and cultural denomination of Tehuelches. The Ona or Selk´nam group (ONA, n = 16) also had a terrestrial hunting-gathering strategy and settled the grasslands in the north of the Isla Grande (Tierra del Fuego). Finally, we included the marine hunter-gatherer group known as Yamana or Yahgan (YAM, n =44), who inhabited the southern shores of the Fueguian archipelago. Fueguian populations entered Isla Grande before 12,000-10,000 BP (Clapperton 1992). With the disappearance of the last land bridges of the Magellan Straits, they probably remained isolated from about 8,000 BP until the European contact. After an extensive examination of the archaeological remains from Beagle Channels' sites Lancha Packewaia and Tunel, Orquera et al. (1987) concluded that marine adaptation developed once those populations were inside the Isla Grande. However, there is no clear explanation as to the origin and development of marine huntinggathering strategy in the Fueguian channels. Contact with Europeans produced a breakdown of the traditional way of life and was the main factor leading to the rapid extinction of all Patagonian groups from the beginning of the 19th century to the middle of the 20th century (García Moro et al. 1997).

Biological and Geographic Distance. In order to estimate the biological distance between the samples, we used three different measures: standardized mean measure of divergence (sMMD) (Sjøvold 1973; Sofaer et al. 1986; Prowse and Lovell 1996), Sanghvi distance (SAN) (Sanghvi 1953), and average taxonomic distance (ATD) (Sneath and Sokal 1973). We also constructed a geographic distance matrix (GEO), with linear distances expressed in kilometers between pairs of localities. In the case of northwest and northeast samples, which included specimens of different regions, geographic punctual location was estimated as the epicenter of the subsample distribution.

Design Matrices. As stated by Sokal et al. (1997), when two theories or hypotheses compete to explain a scientific phenomenon, one can measure the agreement of observable facts with each hypothesis to see which one better fits the observation. Design matrices are proximity matrices created for testing hypotheses

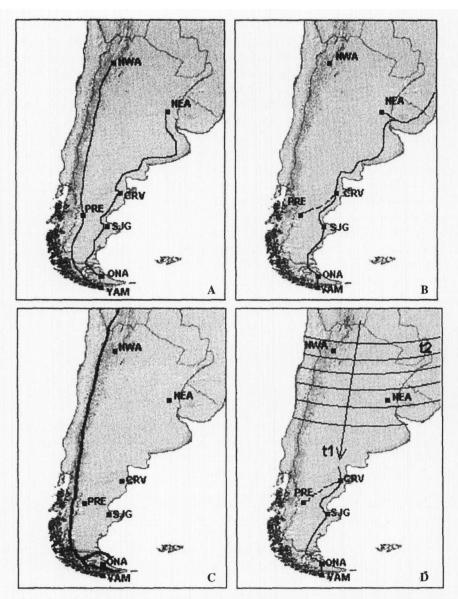


Figure 1. Maps of Argentina and Chile showing geographic location of the seven populations and hypothesized routes involved in the settlement of Patagonia. A: M1, Atlantic-Andean routes; B: M2, exclusive Atlantic route; C: M3, geographic barriers model; D: M4, different ancestors/waves? model; t1: primary hypothetical migration wave; t2: secondary hypothetical migration wave.

about population relationships. A design matrix describes the relative distances among populations expected under a particular model (Waddle et al. 1998). An element of a biological distance matrix, like an element of a design, describes the strength of the link between two populations. In a biological distance matrix that value is obtained after analyzing a set of morphological, genetic, and/or physiological traits and computing dissimilarity indexes. Conversely, in a design matrix, the element's values express hypothesized differences. The actual values assigned to the distances in a design matrix are chosen by the investigator and depend on the hypothesis (Waddle et al. 1998). Construction and handling of design matrices is well described in several papers by Sokal et al. (1992, 1997), Waddle (1994), and Waddle et al. (1998). In this study we constructed four design matrices based on different models of the peopling of Patagonia, in accordance with recent literature and personal observations. Models are quite simple and, of course, can be improved in several ways. Nevertheless, simple models are preferable and easier to express in design matrices. Design matrices are given in Table 1 and are based on the following models.

Table 1. Pairwise Hypothesized Distances under the Models of: An Andean-Atlantic Migratory Route (M1), An Exclusively Atlantic Migratory Route (M2), Geographic Barriers as the Cause of Dissimilarities (M3), and Different Migration Waves/Ancestors? for Northern and Southern Populations (M4)

| Population | M1 | M2 | M3 | M4 |
|------------|----|-----|----|----|
| NWA-NEA | 1 | 1 | 0 | 0 |
| NWA-CRV | 1 | 1 | 0 | 1 |
| NWA-SJG | 1 | 1 | 0 | 1 |
| NWA-PRE | 0 | 1 | 0 | 1 |
| NWA-ONA | 1 | 1 | 1 | 1 |
| NWA-YAM | 0 | 1 | 2 | 1 |
| NEA-CRV | 0 | 0 | 0 | 1 |
| NEA-SJG | 0 | 0 | 0 | 1 |
| NEA-PRE | 1 | 0.5 | 0 | 1 |
| NEA-ONA | 0 | 0 | 1 | 1 |
| NEA-YAM | 1 | 0 | 2 | 1 |
| CRV-SJG | 0 | 0 | 0 | 0 |
| CRV-PRE | 1 | 0.5 | 0 | 0 |
| CRV-ONA | 0 | 0 | 1 | 0 |
| CRV-YAM | 1 | 0 | 2 | 0 |
| SJG-PRE | 1 | 0.5 | 0 | 0 |
| SJG-ONA | 0 | 0 | 1 | 0 |
| SJG-YAM | 1 | 0 | 2 | 0 |
| PRE-ONA | 1 | 0.5 | 1 | 0 |
| PRE-YAM | 0 | 0.5 | 2 | 0 |
| ONA-YAM | 0 | 0 | 1 | 0 |

Model 1 (M1) (Figure 1A). In this model we represent a double route of population spreading in Argentina, from north to south, following either the Andes mountain range or the Atlantic shore. Different morphological patterns (ancestors?) are supposed for the samples placed on the Atlantic side and those located in the Andes. Connection between two samples was set to an arbitrary value of zero if both were on the same route and one if they were on different routes.

Model 2 (M2) (Figure 1B). Model 2 tests the hypothesis that settlement followed an exclusively Atlantic route. Under this hypothesis, groups situated on the eastern margin of the country are connected with a zero, or with a value of one if they are not situated there. In accordance with previous studies (González José et al. 1999), we placed the Pre-Andean sample (PRE) as a branch of the Atlantic stock, with an intermediate distance value (0.5) between the populations pertaining to the Atlantic route and those not. This intermediate position is sustained by the hypothetical effect of isolation by distance and by the fact that Pre-Andean samples could have been subjected to gene flow with Andean populations in at least the last 500 years (González José et al. 1999).

Model 3 (M3) (Figure 1C). Model 3 tests the hypothesis that morphological differences are due to isolation caused by two main geographic barriers: the Andes and the Magellan Straits. In this case, the Yamana group (YAM) is separated from the Ona (ONA) by a distance of 1, and from the remaining populations by a distance of 2. In this manner, each geographic barrier separating two populations implies a sum of one value in its pairwise distance. Obviously, samples not separated by a geographical barrier are connected with a zero.

Model 4 (M4) (Figure 1D). Model 4 tests the hypothesis that northern populations are derived from a different migratory wave (t2 in Figure 1D) than southern ones (t1 in Figure 1D). Thus, Fueguian-Patagonian samples have a common morphological pattern (ancestor?) different from that of the northern populations. A distance of zero was arbitrarily assigned to localities situated in the same migratory wave. Fueguian-Patagonian groups are arbitrarily separated from northern groups by a value of one, in order to maximize the dissimilarity hypothesized under the idea of more than one migratory wave.

Matrix Correlation. Testing such models would require (1) a way of detecting associations between distance matrices, and (2) a way of testing the significance of these associations. The Mantel r statistic was used to evaluate the correlation between the obtained morphological distance matrix, the spatial separation matrix, and the design matrices representing models of Patagonia's human settlement. The Mantel statistic tests the pairwise association of elements of two distance matrices by computing the running total of the element-by-element or Hadamard product of the two matrices. Significance of the correlation was deter-

mined by a permutation test: the rows and columns of one matrix are permuted and the Mantel statistic calculated 9999 times, creating a distribution that is used to evaluate the significance of the observed correlation (Mantel 1967; Smouse et al. 1986; Waddle 1994; Sokal and Rohlf 1995).

Alternatively, the Smouse-Long-Sokal test (Smouse et al. 1986; Oden and Sokal 1992) was 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 $\bf A$ and $\bf B$ is significant when one or more matrices $\bf C, D, \ldots$ are held constant.

Results

Basic data concerning frequencies of the 20 traits studied and the seven populations considered are presented in Table 2. The values of the three biological distance computations and those of the geographical distances are given in Table 3. A dendrogram (Figure 2) resulting from unweighted pair group with arithmetic mean analysis (UPGMA) (Sneath and Sokal 1973) clustering of the sMMD distance matrix represents the relations between the populations in that

Table 2. Skull Incidences of 20 Nonmetric Traits in Seven Cranial Samples from Argentina

| Trait | NWA | NEA | CRV | SJG | PRE | ONA | YAM |
|------------------------------------|-------|-------|-------|-------|-------|-------|-------|
| 1 Ossicle at the lambda | 5/30 | 1/31 | 6/61 | 3/36 | 1/14 | 0/16 | 0/43 |
| 2 Lambdoid ossicle | 23/30 | 12/29 | 36/61 | 23/36 | 6/20 | 2/16 | 7/43 |
| 3 Parietal foramen | 24/31 | 23/33 | 26/68 | 20/37 | 10/16 | 12/16 | 35/42 |
| 4 Bregmatic bone | 1/31 | 0/33 | 1/61 | 0/27 | 0/13 | 0/16 | 0/39 |
| 5 Metopism | 4/32 | 0/33 | 3/70 | 0/38 | 0/16 | 0/16 | 0/44 |
| 6 Coronal ossicle | 13/31 | 3/29 | 13/59 | 1/23 | 2/11 | 1/16 | 0/43 |
| 7 Epipteric bone | 3/27 | 2/29 | 3/66 | 0/36 | 5/15 | 0/16 | 3/43 |
| 8 Parietal notch bone | 9/32 | 8/33 | 14/68 | 2/37 | 2/15 | 0/16 | 2/43 |
| 9 Ossicle at asterion | 13/31 | 13/33 | 8/68 | 3/37 | 2/15 | 1/16 | 2/44 |
| 10 Auditory torus | 15/32 | 20/33 | 0/67 | 0/38 | 0/16 | 0/16 | 0/43 |
| 11 Foramen of Huschke | 18/32 | 8/33 | 29/67 | 12/38 | 1/16 | 3/15 | 10/41 |
| 12 Mastoid foramen absent | 23/32 | 26/33 | 3/68 | 2/38 | 1/16 | 0/15 | 4/43 |
| 13 Posterior condylar canal | 28/32 | 21/30 | 42/59 | 23/36 | 12/15 | 12/15 | 37/43 |
| 14 Anterior condylar canal double | 7/32 | 13/29 | 36/60 | 18/36 | 7/15 | 4/13 | 10/43 |
| 15 Foramen ovale incomplete | 4/32 | 5/32 | 4/64 | 1/38 | 0/15 | 1/16 | 1/43 |
| 16 Foramen spinosum open | 20/32 | 17/33 | 17/66 | 12/38 | 3/15 | 6/16 | 10/40 |
| 17 Zygomaticofacial foramen absent | 12/32 | 18/33 | 3/70 | 6/36 | 3/14 | 4/16 | 12/43 |
| 18 Supraorbital foramen | 19/32 | 13/33 | 51/70 | 22/38 | 11/16 | 9/16 | 15/44 |
| 19 Supraorbital notch | 26/32 | 31/33 | 50/70 | 26/38 | 8/16 | 10/16 | 23/43 |
| 20 Accessory infraorbital foramen | 7/32 | 4/32 | 14/70 | 8/37 | 1/16 | 5/15 | 5/43 |

NWA: northwestern Argentina; NEA: northeastern Argentina; CRV: Chubut River Valley; SJG: San Jorge Gulf; PRE: Pre-Andean; ONA: Ona; YAM: Yamana.

Table 3. Biological and Geographical Distances between the Different Groups

| | sMMD | SAN | ATD | GEO (km) |
|---------|-------|-------|-------|----------|
| NWA-NEA | 1.474 | 1.270 | 0.628 | 1,114 |
| NWA-CRV | 5.896 | 3.133 | 0.941 | 2,111 |
| NWA-SJG | 5.750 | 3.126 | 0.965 | 2,487 |
| NWA-PRE | 4.821 | 3.787 | 1.114 | 2,463 |
| NWA-ONA | 6.395 | 3.782 | 1.024 | 3,270 |
| NWA-YAM | 7.815 | 3.783 | 1.052 | 3,423 |
| NEA-CRV | 7.230 | 3.572 | 0.953 | 1,355 |
| NEA-SJG | 5.437 | 3.064 | 0.856 | 1,767 |
| NEA-PRE | 4.409 | 3.424 | 0.931 | 1,863 |
| NEA-ONA | 5.404 | 3.240 | 0.884 | 2,506 |
| NEA-YAM | 6.073 | 3.201 | 0.867 | 2,658 |
| CRV-SJG | 0.520 | 0.392 | 0.314 | 414 |
| CRV-PRE | 1.052 | 1.127 | 0.521 | 572 |
| CRV-ONA | 2.048 | 1.493 | 0.632 | 1,175 |
| CRV-YAM | 4.209 | 1.989 | 0.716 | 1,329 |
| SJG-PRE | 0.884 | 1.016 | 0.477 | 317 |
| SJG-ONA | 0.521 | 0.895 | 0.401 | 783 |
| SJG-YAM | 1.676 | 1.196 | 0.509 | 941 |
| PRE-ONA | 0.841 | 0.905 | 0.488 | 870 |
| PRE-YAM | 0.837 | 0.947 | 0.473 | 1,023 |
| ONA-YAM | 0.093 | 0.367 | 0.293 | 163 |

sMMD: standardized mean measure of divergence (Sjøvold 1973; Sofaer et al. 1986; Prowse and Lovell 1996); SAN: Sanghvi's Distance (Sanghvi 1953); ATD: average taxonomic distance (Sneath and Sokal 1973); GEO: linear distances in kilometers.

matrix (the same procedure applied to SAN and ATD distance matrices results in the same clustering). A first branching in the dendrogram shows a separation between the northern groups (NWA, NEA) and Fueguian-Patagonians (CRV, SJG, PRE, ONA, YAM). Subsequent division of the latter involves two northern Patagonian samples (CRV, SJG) on one side and the Pre-Andean and Fueguian groups (PRE, ONA, and YAM) on the other. Finally, Fueguian groups appear in the same cluster, showing the minor distance obtained in this study. Results of correlation matrix based on Mantel's statistic are given in Table 4. This table clearly shows that, as expected, the three estimators of distance are congruent separating groups. In fact, Mantel tests are highly significant for all three comparisons between sMMD, SAN, and ATD. An inspection of the same table reveals that correlation of geographic distance (GEO) with all three estimators of biological distance (and with model M4) are significant, showing that about 85% of the nonmetrical variation is due to spatial separation. In order to eliminate the correlation between geography and biological distance, we carried out the Smouse-Long-Sokal test with GEO held constant (Table 5).

Although Table 4 shows that correlations between biological distance and

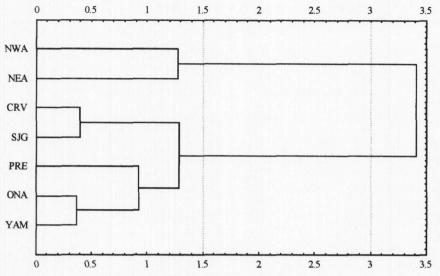


Figure 2. Dendrogram showing the results of UPGMA clustering of the sMMD distances between the seven populations studied.

any of the models are insignificant, when geographic distance is held constant the correlations between sMMD, SAN, or ATD and one of the models (M4) becomes highly significant ($r_{\text{sMMD},\text{M4}} = 0.749$; p < 0.0001) (Table 5).

Discussion

One notable effect in most anthropological studies is the positive relationship between increasing geographic separation and phenotypic or genetic dis-

Table 4. Matrix Correlations between Three Biological, One Geographical, and Five Design (Models) Matrices of Distance

| | sMMD | SAN | ATD | GEO | M1 | M2 | M3 | M4 |
|------|--------------------|--------------------|-------------|--------------------|--------|--------|--------|----|
| sMMD | 0 | | | | | | | |
| SAN | 0.958a | 0 | | | | | | |
| ATD | 0.935a | 0.984^{a} | 0 | | | | | |
| GEO | 0.879^{a} | 0.898^{a} | 0.899^{a} | 0 | | | | |
| M1 | 0.008 | 0.017 | 0.071 | 0.046 | 0 | | | |
| M2 | 0.065 | 0.182 | 0.276 | 0.247 | 0.427 | 0 | | |
| M3 | 0.014 | -0.091 | -0.116 | 0.167 | -0.045 | -0.279 | 0 | |
| M4 | 0.914 ^b | 0.954 ^b | 0.910^{b} | 0.849 ^b | -0.045 | 0.145 | -0.190 | 0 |

a. p < 0.001.

b. p < 0.05.

Table 5. Partial Correlations between Three Biological Distances and Five Models of Peopling, Holding Geography Constant

| | sMMD | SAN | ATD |
|----|--------------------|--------------------|--------------------|
| M1 | 0.081 | 0.069 | -0.041 |
| M2 | 0.397 | 0.189 | -0.004 |
| M3 | 0.324 | 0.566 ^a | 0.618a |
| M4 | 0.749 ^b | 0.859 ^b | 0.717 ^b |

a. p < 0.05.

tance among groups (Konigsberg 1990). According to this view, the isolation-bydistance model forecasts that human subpopulations will reflect geographic separation in the pattern of their between-group biological distances (Wright 1943). The eventual result is a greater genetic similarity between geographically proximal populations and increasing genetic differences between groups that are further and further apart (Crawford 1998). It is a fact that data in this study are strongly geographically patterned, since the correlation between spatial separation and all three estimators of biological distance is the most notable result (Table 4). In agreement with this, Lalueza et al. (1996) proposed that geographic distance (in the latitudinal sense) is the main factor that influenced the differentiation, from a single ancestral population, of human groups from Tierra del Fuego and Patagonia. It is well known that spatial autocorrelation disturbs the error rates of conventional statistics (Cliff and Ord 1981). The most significant aspect of this issue concerns not only the spatial separation, but the spatial distribution of the samples. In fact, the samples are discontinuous in space; two are northern and the remainder southern. We do not include samples from central Argentina. As expected, sMMD, ATD, and SAN are spatially autocorrelated, and because of that we next calculated partial correlations (Smouse-Long-Sokal test) by holding GEO constant. In this way, we tested whether any correlation remained between biological and hypothesized distance matrices, once the correlation due to the regressor variable (GEO) was eliminated (Sokal et al. 1992). Following this procedure, we controlled to the spatial autocorrelations' statistical noise (e.g., a northsouth cline) and accounted for the effect of the models beyond the effect of spatial separation.

A further point needs to be made about temporal separation among the samples. Unfortunately, there is an important lack of chronocultural information about the majority of Argentinean collections. Between-sample temporal distance could be involved as an important determinant of biological distance. However, Konigsberg (1990) demonstrated theoretically and empirically that it is possible to analyze populations that are subdivided in space and by time. In his work, Konigsberg (1990, 65) states that:

b. p < 0.0001.

under a fixed migration pattern (incorporating isolation by distance) there should be positive correlation between genetic distance and spatial distance (controlling for time) and negative correlation between genetic and temporal distance (controlling for space. . . . The increased similarity with increasing temporal separation is due to the homogenizing effect of gene flow.

Following this approach, we can assume that biological distances obtained here are equivalent to *minimum biological distances*, and consequently models can be discussed in reference to observed differences.

Design matrices are a useful tool for exploring the causes of population differentiation (Waddle et al. 1998). Therefore, we have used design matrices to evaluate the explanatory strength of four competing models for the peopling of Patagonia. Model 1 represents a settlement based on two pathways, the Andean route and the Atlantic one. Authors like Rothammer et al. (1984), Cocilovo and Di Rienzo (1984–85), Guichón et al. (1986), and Guichón and Varela (1990) suggested this idea based on archaeological, craniometric, somatometric, and genetic data. Under this model, a greater similarity is expected for samples located along the same route, as illustrated in Figure 1A. However, it seems that nonmetric cranial variation does not support this hypothesis: in Table 5 we clearly observe that partial correlation between biological distance matrices and M1 results in a low, nonsignificant association. In fact, M1 offered the worst explanation for population differences. The first model considered above can suggest one additional model, a pathway for an Atlantic settlement (M2).

An inspection of Tables 4 and 5 indicates that M2 fails to explain morphological affinities, regardless of whether GEO is held constant. It should be pointed out that these results do not seem to agree with those of Mendez and Salceda (1995), who stated that the primitive populations distributed in northeastern and southern Argentina coincided with the first waves of populations with greater mobility from northeast to south.

We constructed M3 to represent a situation in which geographic barriers play an important role in establishing morphological relationships between populations. Since the Andes and the Magellan Straits are the main geographic barriers considered, YAM is expected to be the most differentiated group and ONA to represent an intermediate degree of differentiation. Correlation between biological distances and M3 is not significant; nevertheless, when spatial separation is removed from the analysis, this correlation becomes low but significant ($r_{\text{SAN.M3}} = 0.566$; p < 0.05). Considering that the Smouse-Long-Sokal test requires more conservative significance values to reject the null hypothesis (as discussed earlier), these results indicate that M3 is unable to explain morphological differences. These results also seem to confirm the observations made by Legoupil and Fontugne (1997). Based on archeological data, those authors state that a mixed terrestrial-marine hunting strategy could be the main adaptation of the primitive

settlers of the Magellan Straits. According to the authors, this mixed strategy was possible because in the Magellan Straits border and in the southern Beagle Channel, the Andes are low and communication between the grasslands and the coast is direct. As noted early by Borrero (1994–1995), geographic barriers do not seem to be important in this region.

Interpretations of the patterns of diversity of modern humans cannot ignore whether the morphological variation observed results from differential inheritance of archaic traits by different modern groups or from the process of diversification from an already modern form (Lahr 1995). Considering this, in M4 we propose an arrangement of distances in which northern and southern populations have different ancestors. As viewed in Tables 4 and 5, M4 is strongly associated with the morphological variation, even more so when geographic distance is held constant. It should be stressed that even when M3 shows significant values in Table 5, M4 seems to be more consistent in terms of statistical significance. As stated by Oden and Sokal (1992), using a conservative p-value for the Smouse-Long-Sokal method, say, p = 0.001, one can be reasonably certain that the partial correlation coefficients are significant at p < 0.05. In this context, M4 is the most convincing explanation of the pattern of morphological (nonmetric) variation. In addition, we must remark that models are not correlated (see Table 4). Then, we can assume that models evaluated here are self-explanatory, representing independent approaches, and there is no possibility of confounding the effects of the designs. Unfortunately, no samples were available for populations that inhabited central Argentina, and generalizations about the morphological pattern of these groups cannot be made.

The evidence presented here is in agreement with conclusions of Lahr (1995, 1996), who argued for a morphological heterogeneity within the Amerindians, and placed the Fueguian-Patagonians as a group retaining the morphology of the first settlers of the Americas. Our results also correspond with those of Lalueza et al. (1997). These authors studied the Amerindian mitochondrial DNA lineages in samples of extinct Fueguian populations, and their results allowed them to argue that the ancient inhabitants of Tierra del Fuego may be associated with the first settlers entering America. Probably the most economic way of interpreting these results is to see the Fueguian-Patagonians as the end part of a pre-Mongoloid migration involved in the settlement of the Americas. Neves and Pucciarelli (1990, 1991) and Lahr (1995, 1996) extensively discussed such a possibility in several papers that evaluated the morphological affinities of prehistoric skeletal remains.

As stated by Crawford (1998), the elaborate models used in assessing the genetic structure of the Amerindian population reveal underlying patterns. The morphological proofs presented in this study seem to indicate that the biological affinities of the main aboriginal groups of Patagonia and Argentina, as much as settlement mechanisms, might have been more intricate than envisaged so far.

Future studies using new skeletal series and other classes of morphological,

genetic, or linguistic traits will be needed to evaluate the robustness of these hypotheses. These results raise new and interesting questions about the peopling of the extreme south of America.

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