South Amerindian Craniofacial Morphology: Diversity and Implications for Amerindian Evolution

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ABSTRACT   The most compelling models concerning the peopling of the Americas consider that modern Amerindians share a common biological pattern, showing affinities with populations of the Asian Northeast. The aim of the present study was to assess the degree of variation of craniofacial morphology of South American Amerindians in a worldwide context. Forty-three linear variables were analyzed on crania derived from American, Asian, Australo-Melanesian, European, South-Saharan African, and Polynesian regions. South America was represented by seven Amerindian samples. In order to understand morphologic diversity among Amerindians of South America, variation was estimated using regions and local populations as units of analysis. Variances and F_{ST} values were calculated for each unit, respectively. Both analyses indicated that morphologic variation in Southern Amerindians is extremely high: an F_{ST} of 0.01531 was obtained for Southern Amerindians, and values from 0.0371–0.1205 for other world regions. Some aspects linked to the time and mode of the peopling of the Americas and various microevolutionary processes undergone by Amerindians are discussed. Some of the alternatives proposed to explain this high variation include: a greater antiquity of the peopling than what is mostly accepted, a peopling by several highly differentiated waves, an important effect of genetic drift, and gene flow with Paleoamericans. A combination of some of these alternatives explains at least some of the variation. Am J Phys Anthropol 127:000–000, 2005.   © 2005 Wiley-Liss, Inc.

Hrdlicka (1914) originally proposed that American Indians were a homogeneous substratum, the "American homotype," which arrived from Northeast Asia via the Bering Strait. However, several anthropologists claimed a greater heterogeneity among Amerindians, recognizing at least two main types, "dolichocephalic" and "brachycephalic." One of the most extreme proponents of this was Imbelloni (1939), who suggested that American aborigines comprised 11 types derived from seven migratory waves which originated in Asia and the Pacific. The origin of this variation among American Indians was therefore placed by this author outside America, implying that variation between populations were the result of individual waves of migration. The possible microevolutionary processes that developed among these groups once they entered America were completely disregarded.

The "three-migrations model" (Greenberg et al., 1986) became one of the most widely accepted migration scenarios. This model is based on linguistic, genetic, and dental evidence. According to the dental evidence, it is proposed that 20,000 years ago in Southeast Asia, the "sinodont" dental pattern developed from the "sundadont" type. Sinodonty is characterized by the addition and intensification of specific dental traits, being more specialized than sundadonty. Sinodonty is observed in modern populations of Northeast Asia and the Americas. According to this model, a first wave, associated with the Paleoindian Clovis Culture, entered America around 12,000 years BP and colonized the main part of the continent, giving rise to Amerindians. Around 10,000–7,000 years BP, two other waves entered the continent, giving rise to the Na-Dene and Eskimo groups which occupied the Northwest coast and the circumpolar regions of North America (Greenberg et al., 1986).

The "four-migrations model" was proposed by Neves and Pucciarelli (1989, 1991, 1998). Using craniometrical evidence, these scholars supported the three divisions, and additionally proposed a fourth wave which is the oldest. The first migrants

to America would have entered the continent around 14,000 years BP through the Bering Strait and gave rise to the Paleoamericans, a group that some suggest does not show characteristics of modern northeastern Asians (Neves and Pucciarelli, 1989, 1991, 1998), as modern Amerindians do. The Paleoamerican group, often called Paleoindians, includes all remains dated to about 14,000–9,000 BP (Neves and Pucciarelli, 1989, 1991; Steele and Powell, 1992; Jantz and Owsley, 2001). The term "Paleoindian" is normally employed in the literature to refer specifically to Late Pleistocene/Early Holocene hunter-gatherers from the New World (Meltzer, 1993), and in the chronological sense of the term, all Paleoamericans are also Paleoindians. However, "Paleoamerican" refers to the presence or absence of a set of morphological cranial traits, whereas "Paleoindian" is solely based on chronological-cultural characteristics of a specimen or group of specimens (for a definition of both terms, see Powell and Neves, 1999).

Because some suggested that Na-Dene and Eskimo populations do not represent groups of independent origins (e.g., Szathmáry and Ossenberg, 1978; Szathmáry, 1979, 1993), the four-migrations model was renamed the "two-components settlement system" (Pucciarelli et al., 2003) or the "two main biological components model" (Neves et al., 2003). The two-components model maintains in essence the conceptual division between Paleoamericans and Amerindians, but includes the Na-Dene and Eskimo populations within the Amerindian group. Paleoamericans' ancestors, an Australo-Melanesian-like population, came from Asia and entered via the Bering Strait (Neves et al., 2003). This interpretation of the ancestors of the first Americans could explain similarities found between Paleoamericans and modern Australians (Neves et al., 2003). Even when Amerindians seemed to have occupied the same or a wider geographic range than Paleoamericans, Neves and Pucciarelli (1989, 1991) stated that Paleoamericans did not contribute to the Amerindian gene pool.

The "single-migration model," based on mitochondrial DNA and the Y-chromosome, was independently proposed by different authors. Schurr et al. (1990) indicated that most American aborigines have the A, B, C, and D mitochondrial lineages. According to Merriwether et al. (1995) and Bonatto and Salzano (1997), these lineages form part of a single migration because they are present in all American populations (Schurr et al., 1990; Merriwether et al., 1995; Forster et al., 1996; Bonatto and Salzano, 1997). In general terms, dendrograms show that Amerindian, Na-Dene, and Eskimo groups are closer to each other than to any other Asian group. The origin of the migration was estimated at around 30,000–40,000 years BP. Studies of the Y-chromosome support this model (Pena et al., 1995; Bianchi et al., 1997).

The single-, three-, and four-migrations and two-components models suggest that Amerindians are closer to northeastern Asians due to the geographic origin of the Amerindian ancestor. Furthermore, since Amerindians are descendants of a single migratory wave, they share a common biological pattern. However, some genetic (Parr et al., 1992; Cavalli-Sforza et al., 1994; Easton et al., 1996; Brown et al., 1998), linguistic (Nichols, 1990), and morphologic (Lahr, 1995; Hernández et al., 1997; Brace et al., 2001; Sardi, 2002) studies cast doubts on the Amerindian affinities and diversity proposed by these models. Cavalli-Sforza et al. (1994) assessed levels of genetic variation in different regions and found that the Americas (and in particular, South America) are the most genetically variable part of the world. Similar assessments of craniometrical variation have not been done.

The purpose of this paper is to assess morphologic diversity in South American Amerindians[1] from the analysis of cranial morphology in a worldwide context. We computed F_{ST} values, considering different arrays of samples, and discuss the results in terms of both the characteristics of the initial peopling and the microevolutionary agents which potentially shaped modern diversity.

MATERIALS AND METHODS

Morphologic diversity was evaluated from a geographical point of view. Six worldwide regions were considered, and each region was represented by three cranial samples (Table 1). Data derives from the data set of Howells (1973, 1989). Six South Amerindians samples were also included from data obtained by one of the authors (M.L.S.) (Fig. 1). Three samples represent the Patagonia region: the Chubut River Valley (n = 38 females and 61 males), Rio Negro River Valley (n = 22 females and 41 males), and Fueguians (n = 27 females and 18 males). These groups inhabited the steppe grassland plain extending from central Argentina to the northern part of the Isla Grande of Tierra del Fuego, as well as the channels, fiords, and rugged islands from the southern coast of Tierra del Fuego. They displayed a forager economy, mainly based on the hunting of guanaco which was intensively exploited until nearly historic times in the steppe grasslands, and the hunting of seals and the collecting of shellfish on the shorelines. Two samples come from the Pampean region in central Argentina: the Parana River Delta sample (n = 16 females and 22 males), with an antiquity estimated by archaeological associations at around 2,000 years BP (Torres, 1911), and the Western Pampas sample (n = 20 females and 17 males), which represents a Mapuche population that settled in the Pampas in the 17th and 18th centuries after migrating from the Andean region (Casamiquela, 1990). The Parana Delta remains are associ-

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[1]Amerindians are considered in this study in the sense of the two-components model.

TABLE 1. *List of samples of Howells (1973) considered in this study*

Region	n	Local populations
South-Saharan Africa	283	Teita, Dogon, Zulu
Europe	317	Norse, Zalavar, Berg
Australo-Melanesia	298	Australia, Tasmania, Tolai
Asia	261	Hainan, South Japan, North Japan
Polynesia	294	Moriori, Mokapu, Easter Island
Americas	281	Peru, Arikara, Santa Cruz

TABLE 2. *Cranial measurements considered in this study (from Howells, 1973)*

Glabello-occipital length	Nasio-frontal subtense
Nasio-occipital length	Biorbital breadth
Basion-nasion length	Dacryon subtense
Basion-bregma height	Interorbital breadth
Maximum cranial breadth	Simotic chord
Maximum frontal breadth	Malar length inferior
Bistephanic breadth	Malar length maximum
Bizigomatic breadth	Malar subtense
Biauricular breadth	Cheek height
Minimum cranial breadth	Supraorbital projection
Biasterionic breadth	Glabella projection
Basion-prosthion length	Foramen magnum length
Nasion-prosthion height	Nasion-bregma chord
Nasal height	Nasion-bregma subtense
Orbit height	Nasion-bregma fraction
Orbit breadth	Bregma-lambda chord
Bijugal breadth	Bregma-lambda subtense
Nasal breadth	Bregma-lambda fraction
Palate breadth	Lambda-opisthion chord
Bimaxillary breadth	Lambda-opisthion subtense
Zygomaxillary subtense	Lambda-opisthion fraction
Bifrontal breadth	

Fig. 1. Geographical localization of South Amerindian samples.

ated with the "Cultura Básica del Litoral" which is characterized by a subsistence based on hunting and fishing. The Western Pampas must have acquired the horse somewhere around the early 18th century, and in the middle 18th century, the staple food of this group was horse meat. Bolivians (n = 9 females and 10 males), of Aymará-Quechua origin, derived from the Andean highlands and were subsistence agriculturalists. Potatoes were the staple crop, although quinoa was the most important grain. Further studies on the craniofacial affinities and variation of Patagonian,

Pampean, and Andean groups, as well as their implications for the New World's settlement, can be found in Cocilovo and Di Rienzo (1984–1985), Cocilovo and Neves (1988–1989), Neves (1989), González-José et al. (2001a,b, 2002, 2003), Luis et al. (1999), and Sardi (2002). In a recent study, González-José et al. (2005) provided a complete revision of the archaeological, ecological, and demographic backgrounds for each series, which were used to estimate the potential effects of subsistence strategy on functional cranial components.

Forty-three of the linear variables of Howells (1973) were used in this study (Table 2). Data were size-corrected through the Q-standardization proposed by Darroch and Mossiman (1985). Analyses of cranial shape were done pooling sexes. When sexual dimorphism in shape exists, this affects within-population variation. Given that the smallest unit of analysis of this study is "population" (see below), the variation in each population produced by any factor such as sex is assumed as negligible in among-populations comparisons.

Morphologic assessments were based on a neutral model-bound approach which considers evolutionary parameters that affect the population structure (Williams-Blangero and Blangero, 1989; Relethford and Blangero, 1990). Matrices of distance to the centroid (R-matrices) with two types of units (regions and local populations) were obtained. An R-matrix is the scaled variance-covariance matrix over the total mean of allele frequencies (Harpending and Jenkins, 1973). The r_{ii} value represents the genetic distance of unit i to the centroid, which was obtained with all units. The weighted mean of all r_{ii} is Wright's F_{ST}, which measures the proportion of total variation which corresponds to differences among units. The

greater the F_{ST}, the greater the difference among units (Relethford and Blangero, 1990). Genetic distances can reflect gene flow, genetic drift, or common ancestry (Relethford, 1996). Under a balance of gene flow and genetic drift, the observed variance of unit i and r_{ii} are linearly related. If a unit underwent more gene flow than expected regarding other units, it will show a greater variance. The residual value expresses the difference between the observed and expected variances; positive and negative residuals reflect greater and lesser variances than expected.

The total diversity of a species is the sum of the diversity among and within geographic regions; the diversity within a region is the sum of the diversity among and within local populations of that region (Relethford, 2002). In order to divide the components of morphologic diversity within a region, the apportionment of quantitative variation was done following Relethford (2001, 2002). Regional variance was evaluated from the study of the two units of analysis: the geographic regions and the local populations of each region (among-regions and among-local-populations analyses, respectively). A heritability of 0.55 was assumed (Relethford, 1994). F_{ST} values were corrected for sample bias and were calculated using the RMET program, written by John Relethford.

Among-regions analysis

The variation within a region is deduced from the observed variances and the residuals. Residuals reflect the difference from the expected variance. We considered seven world regions. Six regions listed in Table 1 are the same analyzed by Relethford (2001). In addition, the Patagonia region, comprised of Chubut, Rio Negro, and Fueguian samples, was included. These samples do not show geographical overlap with the American samples of the database of Howells (1973). Each region is represented by three local populations. Patagonia is supposed to have been peopled by a single migratory wave (González-José et al., 2001a). Although some contact with Andean groups was inferred from archaeological assemblages of the Patagonian area (Gómez Otero et al., 1998), intense gene flow was not probable. Furthermore, Patagonian populations never underwent an important demographic growth (Borrero and McEwan, 1997). Thus, a low morphologic variation is expected among them. All South American samples used in the "among-local-populations analysis" (see below) were not included here, in order to avoid an overestimation of regional variance by a greater number of local populations.

Among-local-populations analysis

F_{ST} values are estimators of within-region variation due to differences among local populations within a region. These were calculated on the local

TABLE 3. *Estimates of regional variance after pooling geographic regions as unit of analysis*

|	r_{ii}	Variance	Residual
South-Saharan Africa	0.2097	0.870	0.109
Europe	0.1191	0.824	−0.025
Asia	0.1063	0.816	−0.044
Australo-Melanesia	0.2078	0.742	−0.021
Polynesia	0.1480	0.793	−0.027
Americas	0.0998	0.789	−0.078
Patagonia	0.1536	0.901	0.086

populations of the seven regions previously analyzed. The total South Amerindian variation was assessed, calculating F_{ST} values with Chubut, Rio Negro, Fueguian, Bolivian, Parana Delta, Western Pampas, and Peru samples, in two ways. One F_{ST} was calculated after pooling the seven South Amerindian samples, whereas 35 F_{ST} values were obtained with all possible combinations of three samples taken among the seven previously mentioned. The second approach is oriented to: 1) obtain the F_{ST} with the same number of samples as in the non-American regions, hence ruling out that the great number of samples leads to greater F_{ST}; 2) to detect which combinations show the greatest F_{ST}; and 3) to compare different distributions of F_{ST}.

Local populations from different non-American regions were combined, and distributions of F_{ST} values were obtained to compare them with the South Amerindian distribution. These assemblages were expected to show greater F_{ST} values than those of South America. Since Asia is considered the region from which migrations to America originated, the Amerindian distribution was compared with samples in which Asian groups are combined with groups from other regions (Australo-Melanesia, South-Saharan Africa, Europe, and Polynesia).

RESULTS

In the among-regions analysis, an unbiased F_{ST} of 0.1492 (standard error = 0.0015) and a mean within-region variance of 0.819 were obtained. Patagonia and South-Saharan Africa showed greater variances, which are expressed as positive residuals (Table 3). The outlier position of Patagonia and South-Saharan Africa is shown in Figure 2; also shown is the differentiation of Patagonia regarding the American group.

Table 4 presents the among-local-populations analysis. With the exception of Patagonia, the F_{ST} values are very similar to those obtained by Relethford (2001) from a z-standardized analysis of measurements, in other words, for the size and shape components of morphology. Relethford (2001) found a significant association of among-group differentiation and geographic distance. In this worldwide context, Patagonia occupies the third position after Polynesia and the Americas, reflecting that Patagonian groups show higher variation than those from larger geographical regions.
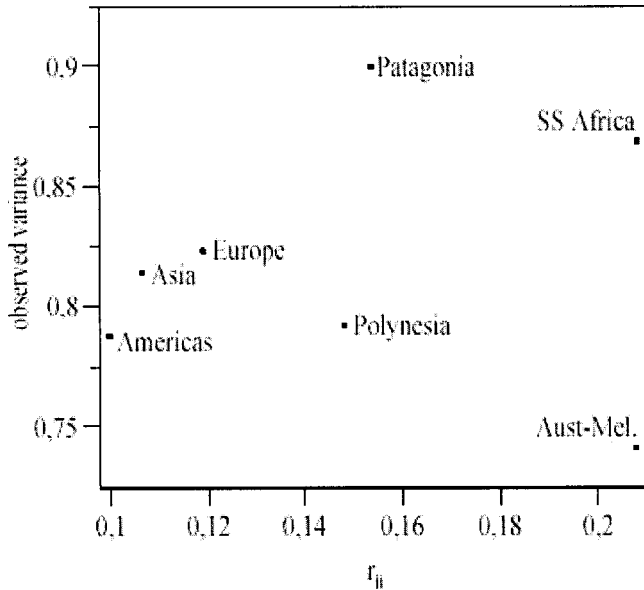
Fig. 2. Plot of world regions according to variance vs. distance to centroid of distribution (r_{ii}). SS, South-Saharan, Aust-Mel., Australo-Melanesia.

TABLE 4. Estimates of regional variance, considering local populations as unit of analysis

	F_{ST} (standard error)	Mean within-region variance
Polynesia	0.1205 (0.0036)	0.836
Americas	0.1005 (0.0036)	0.893
Patagonia	0.0889 (0.0043)	0.926
South-Saharan Africa	0.0825 (0.0035)	0.938
Australo-Melanesia	0.0686 (0.0030)	0.924
Europe	0.0549 (0.0027)	0.925
Asia	0.0371 (0.0026)	0.961

With the seven South American samples, an F_{ST} of 0.1531 (standard error = 0.0038) was calculated, with a mean within-population variance of 0.898. The morphological relationships are expressed in the plot of the main eigenvectors obtained with the matrix of similitude among samples (Fig. 3). The closer samples are those of Patagonia, followed by Bolivians, Peru, and the Western Pampas. The Parana Delta sample is the most distanced.

All combinations of three South American samples taken among the seven ones produced 35 F_{ST} values (Table 5). These values are normally distributed, as tested by a Kolmogorov-Smirnov analysis where the maximum difference (0.0689) has a nonsignificant probability. The minimum F_{ST} is that of Patagonia (Chubut, Rio Negro, and Fueguians) (0.0889); the maximum (0.2181) is that for the combination of the Western Pampas, Parana Delta, and Peru. The mean of the distribution is 0.1550, with a standard deviation of 0.0313. F_{ST} values for the geographically closest populations are: 0.1350 for Chubut, Rio Negro, and Parana Delta; 0.1619 for Chubut, Rio Negro, and Western Pampas; 0.1796 for Rio Negro, Parana Delta, and Western Pampas; and 0.2034 for Chubut, Parana Delta, and Western Pampas. Note
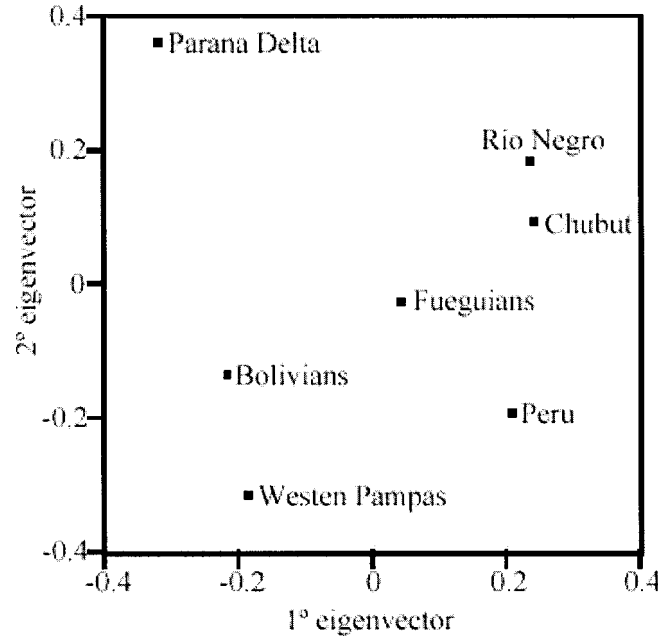
Fig. 3. Plot of morphologic relationships between seven South Amerindian samples. First two eigenvectors account for 58.4% of total variance.

that the average of the distribution (0.1550) is almost equal to the F_{ST} (0.1531) which represents the average of distance to the centroid after pooling the seven samples. This reflects that distances to the centroid are normally distributed, which is expressed in the normal distribution of the 35 F_{ST}. This indicates that F_{ST} values are not inflated by the presence of one sample highly differentiated with respect to the others, which would modify the shape of the distribution. The greatest F_{ST} values are produced in the comparisons of Parana Delta, moreover when this sample is associated with Peru and Western Pampas (Table 5). This is in accordance with its high differentiation shown in Figure 3.

Table 6 gives descriptive statistics for the distributions of F_{ST} values resulting from the combination of Asian populations with other non-Amerindian samples. The only combination that shows a greater differentiation than the mean of Amerindians is that of one Asian population with two Australo-Melanesian ones. Values close to the average of Amerindians are found when Asian groups are combined with one Australo-Melanesian population (and the pooled distribution), with two Polynesian groups, and with two African groups.

DISCUSSION

The low variation observed among Patagonian populations when compared to other Amerindians (Table 5) would be in accordance with the suggestion, based on nonmetric traits, of their unique origin (González-José et al., 2001a). However, the Patagonian assemblage shows the second and the third highest variations in a worldwide context

TABLE 5. Distribution of F_{ST} values calculated with all possible combinations of three South Amerindian samples taken among seven samples

Samples	F_{ST} (SE)	Mean within-populations variance
Chubut, Fueguians, R. Negro[1]	0.0889 (0.0043)	0.926
Chubut, R. Negro, Peru	0.0937 (0.0034)	0.883
Fueguians, Bolivians, W. Pampas[2]	0.1136 (0.0067)	0.952
Chubut, Fueguians, Peru	0.1207 (0.0042)	0.905
Fueguians, W. Pampas, Peru	0.1248 (0.0051)	0.951
Fueguians, R. Negro, Peru	0.1280 (0.0045)	0.915
Fueguians, R. Negro, Bolivians	0.1314 (0.0065)	0.967
Chubut, Fueguians, Bolivians	0.1330 (0.0065)	0.993
Fueguians, Bolivians, Peru	0.1335 (0.0063)	1.005
Chubut, R. Negro, Parana D.[3]	0.1350 (0.0052)	0.880
Chubut, Fueguians, W. Pampas	0.1351 (0.0052)	0.939
Fueguians, R. Negro, W. Pampas	0.1421 (0.0054)	0.911
Fueguians, R. Negro, Parana D.	0.1460 (0.0056)	0.900
Chubut, Fueguians, Parana D.	0.1461 (0.0054)	0.892
Chubut, R. Negro, Bolivians	0.1462 (0.0070)	0.986
Fueguians, Bolivians, Parana D.	0.1528 (0.0070)	0.947
R. Negro, Bolivians, Parana D.	0.1565 (0.0068)	0.960
R. Negro, W. Pampas, Peru	0.1580 (0.0052)	0.921
Chubut, W. Pampas, Peru	0.1604 (0.0050)	0.918
Chubut, R. Negro, W. Pampas	0.1619 (0.0055)	0.921
Chubut, Bolivians, Parana D.	0.1637 (0.0066)	0.948
Fueguians, W. Pampas, Parana D.	0.1675 (0.0062)	0.892
Bolivians, W. Pampas, Peru	0.1690 (0.0064)	1.021
Chubut, Bolivians, Peru	0.1703 (0.0064)	0.972
R. Negro, Bolivians, Peru	0.1712 (0.0066)	0.983
R. Negro, Bolivians, W. Pampas	0.1720 (0.0065)	0.955
Fueguians, Parana D., Peru	0.1786 (0.0055)	0.901
R. Negro, W. Pampas, Parana D.	0.1796 (0.0060)	0.883
Chubut, Bolivians, W. Pampas	0.1842 (0.0063)	0.994
Chubut, Parana D., Peru	0.1850 (0.0051)	0.855
R. Negro, Parana D., Peru	0.1890 (0.0052)	0.878
Bolivians, W. Pampas, Parana D.	0.2005 (0.0073)	0.936
Chubut, W. Pampas, Parana D.	0.2034 (0.0059)	0.885
Bolivians, Parana D., Peru	0.2108 (0.0064)	0.971
W. Pampas, Parana D., Peru	0.2181 (0.0058)	0.905

[1] Rio Negro.
[2] Western Pampas.
[3] Parana Delta.

TABLE 6. Descriptive statistics of distributions of F_{ST} values, comparing Asians with another non-Amerindian samples[1]

	Samples compared		
	2 Australo-M.[2] + 1 Asian	1 Australo-M. + 2 Asian	Pooled
Mean	0.1720	**0.1609**	**0.1665**
SD	0.0272	0.0263	0.0266
Maximum	0.2093	0.2157	0.2157
Minimum	0.1315	0.1285	0.1285
	2 Polynesian + 1 Asian	1 Polynesian + 2 Asian	Pooled
Mean	**0.1494**	0.1318	0.1406
SD	0.0178	0.0179	0.0195
Maximum	0.1783	0.1656	0.1783
Minimum	0.1265	0.1130	0.1130
	2 European + 1 Asian	1 European + 2 Asian	Pooled
Mean	0.1059	0.1049	0.1054
SD	0.0114	0.0093	0.0101
Maximum	0.1200	0.1185	0.1200
Minimum	0.0890	0.0890	0.0890
	2 African + 1 Asian	1 African + 2 Asian	Pooled
Mean	**0.1490**	0.1300	0.1395
SD	0.0123	0.0147	0.0164
Maximum	0.1699	0.1517	0.1699
Minimum	0.1335	0.1077	0.1077

[1] Numbers in bold indicate distributions that fall within confidence limits at $P = 0.95$ of Amerindian distribution of F_{ST} values.
[2] Australo-Melanesian.

(Tables 2 and 3), which is due to the divergence of the mean values of local populations. The closest geographical populations, like those from the north of Patagonia and central Argentina, have higher F_{ST} values than Polynesia, which is the largest geographic region (Table 5). Ross et al. (2002) found an F_{ST} of 0.242, with a heritability of 0.55, indicating high differentiation among Amerindians coming from Central America and northern South America, but the authors included samples with a high European and African component. In this study, distributions of F_{ST} values closer to that of Amerindians can only be attained when Asian populations are grouped with populations from a different region, like Australo-Melanesia, Africa, or Polynesia (Table 6). The maximum F_{ST} among non-Amerindian populations (0.2157) does not reach the highest value (0.2181) obtained for some

South Amerindian samples (Table 5). Gene flow with Europeans must be discarded. A previous study on morphologic distances suggested no affinities between the European and Amerindian groups included in the present work, even for the Western Pampas sample, which is from historic times (Sardi, 2002). Therefore, Amerindians are far from being a homogeneous group in terms of cranial morphology (Tables 2–4).

These results are in accordance with those of Cavalli-Sforza et al. (1994), based on gene frequencies. The literature lacks studies which assess the degree of morphologic variation of Amerindians in comparison with other regions. Some regional studies found associations between morphologic, linguistic (Marcellino et al., 1978; Salzano, 1984), and geographic (Cocilovo and Di Rienzo, 1984–1985; Rothhammer and Silva, 1990) distances in South Amerindians. Lahr (1995) and Hernández et al. (1997) deduced some degree of variation among American Indians by means of analysis of Patagonian populations. Both studies pointed out that Patagonians are not closest to northern Asian populations, as are other Amerindians, and that they show specific traits attributed to selective factors. They proposed that Patagonians have a "generalized" morphology in contrast to the expected

northeastern Asian-like morphology. Facial flatness and sinodonty characterize the native populations of Northeast Asia, known as the mongoloid phenotypic pattern (Lahr, 1995; Hanihara, 2000), but facial flatness has not been observed among Amerindians (Hanihara, 2000; Sardi, 2002).

Two complementary explanations can be advanced to understand the high variability in South Amerindians. One concerns the time and mode of the peopling of the Americas, and the other, the probable microevolutionary mechanisms undergone by populations inside America.

Time and mode of the peopling

Morphologic diversity can be the final result of a greater antiquity of the peopling than that suggested by the three- and four-migrations models and/or by the arrival of several waves of migration from different geographic origins. Beringia, which includes the Bering Strait and adjacent islands (Hoffecker and Elias, 2003), is widely regarded as the main if not only route to enter the Americas. Its occupation must be interpreted in the light of previous estimations about the peopling of Northern Asia, and it appears to have fluctuated in response to climatic change. Northern Asia was occupied between 40,000–28,000 years BP and abandoned between 24,000–21,000 BP, at the time of the Last Glacial Maximum, being occupied again after 21,000 BP when the ice melted (Goebel, 1999; Hoffecker and Elias, 2003). Beringia developed as a land bridge between Northern Asia and Northwest America between 28,000–13,000 BP, when sea levels receded. During the reoccupation of Northern Asia, Beringia was peopled for the first time, as it certainly appeared to be a favorable landscape in terms of climate and resources (Hoffecker and Elias, 2003). The oldest archaeological site in the Tanana Basin of Central Alaska is dated to 14,000–13,400 cal BP (Hoffecker and Elias, 2003). Thus, supporters of the three- and four-migrations models suggest that the migration to the Americas via Beringia was after 14,000 years BP and not before, due to the lack of undoubted earlier evidence in Beringia or America.

After the entry through Beringia, people migrated to occupy all regions of the Americas, with the peopling of South America obviously later than that of North America. However, North America was covered by ice sheets in the Late Pleistocene, casting doubts on the possibility of being occupied at that time (Hoffecker and Elias, 2003; Meltzer, 2003). An internal corridor began to develop between the Laurentide and Cordilleran glaciers about 11,500 BP, but it remained uninhabitable for a long time (Meltzer, 2003). The lack of close similarities between the archaeological remains recovered in Beringia and those of comparable age in North America suggests a different interpretation of the migration process, as previously suggested (Hoffecker and Elias, 2003). Furthermore, the recognition of the site of Monte Verde in Chile as old as 12,500 BP (15,000 cal BP) (Meltzer et al., 1997; Dillehay, 2000) and the presence of other archaeological sites in South America dated at the end of Pleistocene (Cardich, 1984; Dillehay, 2000; Ramírez Rozzi et al., 2000) imply that the mobility of the first Americans was extremely high, to cover the two extremes of the continent in much less than 1,000 years.

A possible migration via Pacific coastal movements was invoked to explain the absence of older sites in North America (Gruhn, 1994; Dixon, 2001). Dixon (2001) offered geological and paleoecological evidence to document the existence of ice-free areas along the Pacific coast where people could have lived. In contrast, Meltzer (2003) believed that the North American coastal route was not habitable until 13,000 BP because ice extended to the outer edge of the continent. This implies that the migration from the North American coast to the Monte Verde site was done in 500 years or in 1,000–1,500 years from Beringia to Monte Verde, i.e., a distance of about 15,000 km. Since there is no solid archaeological evidence on the northern coast of an age older than Monte Verde, it was proposed that archaeological sites were submerged under the sea once the ice sheets melted (Gruhn, 1994; Dillehay, 1999; Dixon, 2001).

The presence of human settlements in the Americas prior to 20,000 BP was suggested by many authors (e.g., Guidon and Delibrias, 1986; Nichols, 1990; Rogers et al., 1992; Gruhn, 1994; Watanabe et al., 2003). However, at the relevant archaeological sites which suggest this old entry to the Americas, the association between human artifacts and faunal remains of extinct Pleistocene species, the anthropic origin of archaeological remains, and the association between artifacts and geological beds are uncertain (Dillehay et al., 1992; Lynch, 1990).

Some genetic studies, based on mtDNA analysis, also estimated an age for the migration to the Americas or the Amerindian differentiation to be older than 20,000 BP (Roychoudhury, 1978; Torroni et al., 1994; Merriwether et al., 1995; Forster et al., 1996; Bonatto and Salzano, 1997). Given that Beringia was unoccupied before that time, these results suggest that Amerindian ancestors started this genetic differentiation regardless of their localized geographical position.

For the single-, three-, and four- (and two-components) migration models, there is only one geographical center for the origin of the Amerindians (Northeast Asia), and the intervention of people from other regions is excluded. However, closer affinities between Amerindians and northeastern Asian people are not accepted by all (see Howells, 1989; Li et al., 1991; Hanihara, 2000; Brace et al., 2001). Amerindian morphology could be a function of Asian diversity during the Pleistocene rather than of diversity in modern times. Indeed, a generalized morphology, distinct from the Mongoloid phenotypic

pattern, was described for the Upper Cave crania of Zhoukoudien (Kamminga and Wright, 1988). Although these crania are variable, in some ways they show affinities with Polynesians and Australo-Melanesians (Cunningham and Jantz, 2003). According to the four-migrations model, the Upper Cave crania of Zhoukoudien have their American counterpart in Paleoamericans (Neves and Pucciarelli, 1998) but not in Amerindians.

It was advanced that the morphologic variation of people inhabiting Siberia or Beringia could probably explain the high variation observed in Amerindians. However, this variation is not highly expressed until the Early Holocene, when people with pronounced and less pronounced Mongoloid traits, resulting from gene flow with Caucasoid or European-like populations, inhabited these regions (Kozintsev et al., 1999). Thus, Siberian diversity cannot be seen as the source of Amerindian diversity.

Genetic studies support the Asian origin of American Indians (Nei and Roychoudhury, 1993; Deka et al., 1995; Crawford et al., 1997; Bonatto and Salzano, 1997; Malhi et al., 2002; Eshleman et al., 2003). However, there is no consensus about the geographic placing of the ancestor. Mongolia, Manchuria, and Siberia were proposed (Neel et al., 1994; Forster et al., 1996; Merriwether et al., 1996). Lately, a new mitochondrial lineage X was identified, which shows an extensive distribution in America (Brown et al., 1998; Malhi et al., 2001; Eshleman et al., 2003) and is absent in East and Central Asia. However, it was recently documented among the Siberian Altaians of South-Central Siberia (Derenko et al., 2001).

Data from parasitologic studies question the unique migration through Beringia. Intestinal parasites found in pre-Columbian Amerindians which originated in the Old World are sensitive to cold and humid climates like that of Beringia (Gonçalves et al., 2003). Thus, they should have arrived by an alternative warmer route.

To summarize the evidence about the peopling of the Americas and the evolution of Amerindians, Amerindians show the closest genetic affinities with Asian populations; the peopling of Beringia occurred in the Late Pleistocene after the Last Glacial Maximum about 14,000–13,400 years BP; and South American sites are older than North American sites. If Beringia has to be considered the only route of entry, regardless of coastal or terrestrial migration route, there is an important gap between the genetic and archaeological estimations for the arrival of Amerindian ancestors. If the morphologic diversity originated outside America, a direct correlate with the diversity of Northeast Asia is absent, regardless of time of entry.

Microevolutionary mechanisms

If the double-migratory event (Paleoamerican and Amerindian) is accepted, the possible representation of Paleoamerican morphology among modern Amerindians has to be considered. The morphologic divergence between Paleoamericans and Amerindians leads us to think that the first wave did not contribute genetically to the second wave (Neves and Pucciarelli, 1989, 1991; Steele and Powell, 1992, 1994; Jantz and Owsley, 2001). In contrast, Powell and Neves (1999) proposed that the divergence can be explained by one migratory event in which the founder population (Paleoamericans) underwent an extreme change by genetic drift, developing the Amerindian morphology. However, González-José et al. (2003) showed that the Amerindian Pericúes of Baja California (Mexico) display a Paleoamerican-like morphology, and suggested that they represent a survival group of Paleoamericans who did not undergo gene flow with Amerindian groups.

There is a good archaeological record during the Terminal Pleistocene of South America. The lithic technology seems not to be derived from the North American Clovis technology (Dillehay, 1999). Moreover, archaeological assemblages in South America reflect high levels of diversity, adapted to each particular environment. What factors could trigger this geographic expansion and diversity? Dillehay (1999), who assumed peopling by a rapid movement along the Pacific coast between 14,000–12,000 BP and by waterways inside America, proposed that environmental change in the Pleistocene-Holocene transition must be seen as the primary cause. The climate became cooler and drier around 12,000 and 10,000 BP, and populations would have limited their mobility and have become differentiated. This proposition implies that the first Americans had high mobility and also extremely good adaptability, which means a high capacity to adapt culturally or biologically to new environments when empty spaces were colonized.

To understand the colonization of empty regions, Surovell (2000) proposed that one must deal with three requirements: the path of the movement, the migration rate, and the reproduction rate. Surovell (2000) arrived at an important conclusion: it is possible that mobile hunter-gatherers have high fertility rates, which may have been the case of the first Americans. But this conclusion has one condition: that diet is held constant within a homogeneous environment, which seems not to have been the case in the initial colonization of South America (Dillehay, 1999).

The high morphologic diversity can also be interpreted in a microevolutionary perspective by the following options: a) greater effective population size, b) greater rate of population growth, c) greater degree of temporal and spatial isolation, as proposed by the genetics-neutral models, and d) adaptative factors, giving importance to environment in shaping cranial morphology.

Options a and b do not seem probable. Rogers et al. (1992) suggested that hunter-gatherers very

rarely increase their population size in short periods of time, and even less during an environmentally unstable period, such as the Late Pleistocene and Early Holocene. Steele et al. (1998) developed a model for Paleoamerican dispersion in North America during the Pleistocene-Holocene transition. Based on modern hunter-gatherer behavior, they assumed a fast population movement and a complete adaptation to resources in the new habitat. Even if many of the assumptions made by this model are not probable, the authors estimated that Paleoamerican dispersion was not followed by a demographic increase.

Option c is partially linked to small population size. The archaeological record shows evidence of occupation in many parts of South America during the Terminal Pleistocene where unstable environmental conditions would inhibit mobility to some degree (Dillehay, 2000). It is probable that a high dispersion in unstable and diverse environments would contribute to morphologic variation through genetic drift in geographically close groups. A smaller population size and greater degree of isolation was also proposed by Deka et al. (1995) to interpret the great F_{ST} values for DNA among American Indians. The genetic distances in America seem not to be correlated with linguistic or geographic distances (O'Rourke et al., 1992; Cavalli-Sforza et al., 1994; Smith et al., 2000; Keyeux et al., 2002); this is more accentuated in South America. According to Templeton et al. (2001), when a homogeneous ancestral population is suddenly fragmented into many small isolated units, one can expect a pattern of no association of geography and genetic distances.

But how much can genetic drift modify morphology in a short period of time? Australia offers some evidence to interpret the potential microevolutionary mechanisms of the Amerindians.

Australia and the adjacent islands were peopled at least by about 40,000 BP or even before (Lourandos, 1997). There is archaeological evidence for a human presence before the Last Glacial Maximum all around this region, supporting the occupation of tropical and temperate habitats. The climate became colder and drier at 25,000 BP, and populations were contracted into refuges near waterways; that is to say, populations became fragmented. In the Late Pleistocene, as the climate ameliorated, the demographic size and the number of sites increased. With the increase of sea level around 12,000–10,000 years BP, Tasmania was isolated without contacts throughout the entire Holocene period. Tables 2 and 3 show a lower variance for this region. Similarly, Lahr (1996) found a low level of variation for morphologic characters, and proposed that the early and long isolation caused the fixation of some characters and the similarity among them. It should be questioned why Australia, where the population range became fragmented during 10,000 years and with the complete isolation of Tasmania in the last 10,000 years, has one of the lower regional diversities, in contrast with America. In other words, why did genetic drift cause low diversity in Australia, while in the Americas it resulted in the highest level? Again, in the American case, one must deal with the diversity of the wave (or waves) of migration.

Option d is seldom invoked. Rothhammer and Silva (1990) found that climate and altitude are lesser associated with craniometrical variation than are geographic distances. Lahr (1995) and Hernández et al. (1997) attributed some characters in Patagonians to the result of an adaptation to cold climate and masticatory stresses. Metric traits present lower transmissibility than nonmetric traits (Cheverud and Buikstra, 1982; Devor et al., 1986a,b), but many studies (Cheverud, 1988; Buikstra et al., 1990; Marroig and Cheverud, 2001) stated that phenotypic distances are proportional to genetic ones. Although the validity of craniometric data is highly criticized because it appears to add environmental "noise," any literature assessing the degree to which environment modifies morphologic distances is lacking. Moreover, Relethford (2002) found a strong similarity among genetic and craniometric results. In other words, the contribution of morphologic adaptation to inflate or reduce distances among populations has not been shown. The effect of environmental factors to promote morphologic variation is not denied; however, some South Amerindians groups with a similar economic strategy, inhabiting close geographic regions (e.g., Chubut, Rio Negro, and Parana Delta), and who were foragers, present a higher F_{ST} (0.135) than non-Amerindians groups (Tables 3 and 4). Thus, it is unlikely that environmental differences have more important effects in America than in any other region of the world.

CONCLUSIONS

South American native populations show a higher degree of craniometrical variation, even when compared to geographically close groups. If we accept that this high variation was due to microevolutionary processes within America, a low population size with high levels of dispersion and fragmentation of the geographic range can be invoked. If the distinction of Paleoamericans is accepted, according to the four-migrations or two-components models, the diversity among Amerindians may have increased due to the genetic contribution of ancient Paleoamericans to the most modern Amerindian groups.

High variation can be also explained by a greater antiquity of the peopling of the Americas or as a result of peopling by two or more Amerindian ancestral waves displaying high morphological diversity. However, one must deal with the lack of conclusive evidence that the peopling occurred

earlier than 13,000 BP or that Amerindians have more than one ancestor, i.e., a non-Asian one.

None of the alternatives mentioned above can explain the high morphologic variation in South Amerindians alone, making it possible that a combination of some or all of the alternatives better explains the heterogeneity observed among South Amerindian populations. The high craniometrical variation found in this study does not solve the problem of their evolution, but contributes to the discussion. These results suggest that any theories which attempt to explain the evolution of Amerindians need to take into account the significant degree of biological variation for this group.

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