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The asymmetry of dermatoglyphic finger ridge counts and the geographic altitude of the Jujenean population in northwest Argentina

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ABSTRACT

Asymmetry is omnipresent in the living world and therefore is a measure of developmental noise and instability. The main stressing agent in high-altitude ecosystems is hypobaric hypoxia. The variation in bilateral dermatoglyphic symmetry in populations from the Province of Jujuy in northwest Argentina is analyzed, and these results are compared to those for other populations with different ethnic and environmental backgrounds. Fingerprints were collected from 310 healthy students (140 males and 170 females) aged 18–20 years from three localities in Jujuy Province—Abra Pampa (3484 m above sea level), Humahuaca (2939 m above sea level), and San Salvador de Jujuy (1260 m above sea level). Asymmetry by sex was assessed based on radial and ulnar ridge counts to determine its pattern of variability (directional asymmetry [DA], fluctuating asymmetry [FA] and antisymmetry), and asymmetry and diversity indices were calculated. A bivariate plot and principal component analysis (PCA) were used to compare these indices with those for other populations. Homogeneity was found between populations and sexes when radial and ulnar ridges were counted. FA values did not show significant differences by locality or side (ulnar and radial), but significant differences were found by finger and sex, with males showing significantly greater FA values. The asymmetry and diversity indices clearly group the Andean populations and separate them from populations of different ethnic and geographic origin. Only the diversity index showed significant differences by locality in males, which suggests a substantially different genetic component in Abra Pampa male samples.

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Introduction

Asymmetry and symmetry are omnipresent in the living world. As vertebrates, humans have bilateral symmetry (Graham et al., 2010). However, a detailed and meticulous corporal examination reveals bilateral asymmetries. Many scientific disciplines, such as anthropology, anatomy, and psychology, study body symmetries and asymmetries (Buchwald and Grubska, 2012). Following the seminal works of Holt (1952) and Jantz (1978), dermatoglyphic morphology has become one of the most studied aspects of symmetry/asymmetry in humans. A detailed review of the topic of dermatoglyphic asymmetry studies has recently been conducted by Buchwald and Grubska (2012).

Fluctuating asymmetry (FA) is defined as small, random deviations from perfect symmetry of the average individual that presumably reflect residual variations after all the direct effects of genotype and environment on traits have been removed (Mather, 1953). FA is also defined as the random variation in the quantitative difference between the right (R) and left (L) sides of a bilateral trait, where the variation is normally distributed about a mean of zero (Palmer, 1996; Van Valen, 1962).

When total phenotypic variation of a trait is divided into genetic and environmental components, FA mainly appears with the random part of the environmental component (Graham et al., 2010). Therefore, FA has become a commonly used measure of developmental precision (Palmer, 1996; Palmer and Strobeck, 2003).

Developmental stability is the capacity of an individual to correct for random perturbations caused by developmental noise (random variation in a suite of developmental factors that are the ultimate cause of subtle deviations from symmetry). Conversely, developmental instability is a suite of processes that tend to disrupt precise development. Increased developmental noise yields lower developmental precision and increased FA (Palmer and Strobeck, 2003).

Directional asymmetry (DA), the normal distribution of R minus L trait values with non-zero mean, is another type of pattern of bilateral asymmetry. DA indicates that a bilateral trait is more developed on one side than the other (Dittmar, 1998). The terms FA and DA refer to patterns of variation in a particular trait exhibited by a sample of individuals.

Dermatoglyphics refers to multifactorial polygenic inheritance traits that are influenced by the environment; these traits develop in the first few months of fetal life. Therefore, both genetic and environmental factors affect their formation during the early stages of prenatal development. During this period, they may also be affected by environmental factors that modify the normal development of the individual. Once formed and in the absence of lesions, these ridges will remain essentially unchanged throughout the life of the individual and therefore are not affected by the environment. They are fixed early in development and consequently are not sensitive to body size variation or age. In addition, the ridges count is a meristic (from Greek "*meristos*" meaning "divided", segmented) trait; that is, ridges are easy to count with little or no error. They also exhibit moderate variation between sides, and counts are independent (or nearly independent) of body size and age, making them an ideal trait for FA studies (Palmer, 1994).

Although a genetic component exists in the asymmetric variation between hand dermatoglyphs, it is larger in DA and less significant in FA, and environmental factors are more important (Karmakar et al., 2013). As symmetry is adaptive (Graham et al., 2010), FA may constitute a developmental response or channeling of environmental change and is therefore indicative of overall developmental homeostasis (Graham et al., 2010; Jantz and Webb, 1980). From this perspective, and concerning multiple bilateral body traits, including dermatoglyphs, several studies have been conducted in order to establish an association between a developmental instability, symmetry, and different disease and health conditions (Buchwald and Grubska 2012; de Bruin et al., 2014; Milnea et al., 2003; Van Dongen, 2006; Van Dongen and Gangestad, 2011; Vilahur et al., 2012).

The main stressing agent in high-altitude ecosystems is hypobaric hypoxia, which affects cell metabolism and causes morphological and functional, hematological, muscular, respiratory, brain, cardiovascular and hormonal changes that impact human growth and development (Beall, 2006). The population of Jujuy Province in northwestern Argentina in the Andean foothills is distributed over an altitudinal gradient between 500 m and > 4000 m and has a composition of 33% European ancestry, 65% Native American ancestry, and 2% African ancestry (Avena et al., 2012). Based on different genetic markers, several studies on the genetic diversity of the province have found that Native American ancestry is more common the higher the altitude above sea level (Dipierri et al., 1998, 2000; Gómez-Pérez et al., 2011, 2013). However, even though immigrants tended to settle at lower altitudes, there is a significant genetic admixture in Jujuy Province.

Adverse environmental conditions may cause an increase in FA, and because it is not affected by the degree of inbreeding and is not very heritable, the amount of variation can be used as an indirect measure of population fitness (Graham et al., 2010; Karmakar et al., 2013; Mukherjee, 1990). As an indicator of environmental stress, FA in different soft and skeletal parts of the human body in contemporary, extinct, and fossil human populations has been analyzed (Albert and Greene, 1999; Bailit et al., 1970; Barrett et al., 2012; Schlager and Rüdell, 2015; Tomaszewska et al., 2015). The precedent analysis of FA and DA in a high-altitude Aymaran population in Northern Chile offers the possibility of comparing this population with the population in Jujuy to assess the effects of high-altitude hypoxic stress on intrauterine dermal ridge formation during prenatal development (Dittmar, 1998). From this perspective, the variation in finger ridge bilateral symmetry in the population of Jujuy living at different altitudes is analyzed, and the results are compared to those found for other populations with different ethnic and environmental backgrounds.

The aim of this paper was to: (1) analyze the variability of ridge count by finger, side, sex, and population according to an altitudinal gradient, (2) establish the pattern of bilateral asymmetry by finger, side, sex, and population according to an altitudinal gradient, and (3) assess asymmetry and diversity indices by sex and population according to an altitudinal gradient in the Jujuy samples and compare them with those obtained for other populations.

Materials and methods

Samples

Fingerprints were collected from 310 healthy students aged 18–20 years (140 males and 170 females) from three localities at different altitudes in Jujuy Province. Of the participants, 86 were from Abra Pampa (3484 m above sea level), 125 were from Humahuaca (2939 m a.s.l.), and 99 were from San Salvador de Jujuy (1260 m a.s.l.). These populations are representative of the altitudinal gradient that orographically characterizes Jujuy Province. The participants provided written informed consent before the commencement of the study, which was approved by the Commission of Bioethics at the Ministry of Health of Jujuy Province.

Dermatoglyphic counts

Fingerprints of both hands were obtained by the classical method of impregnating the epidermis with ink and rolling the fingers on paper. The dermatoglyphic patterns were classified into arches (A), ulnar loops (UL), radial loops (RL), and whorls (W) (Penrose, 1968) and ulnar and radial counts by finger were determined for each individual (Cummins and Midlo, 1961; Holt, 1968).

Asymmetry analysis

We assessed the pattern of between-sides variation in a sample of individuals based on the difference in ridge counts between homologous fingers. For this, we employed the definitions in Van Valen (1962) and Palmer (1994):

> *Fluctuating asymmetry (FA)* is a pattern of variation of the difference between the R and L sides where the variation is normally distributed about a mean of zero.
> *Directional asymmetry (DA)* is a pattern of variation of (R–L) where the variation is normally distributed about a mean that is significantly different from zero.
> *Antisymmetry* is a pattern of bilateral variation in a sample of individuals, where a statistically significant difference exists between sides, but where the side that is larger varies at random among individuals.

In addition, two indices to measure asymmetry—the index of asymmetry and the index of diversity—were used, each providing slightly different information. The results were compared with those for the Aymara population and the other populations considered in the work of Dittmar (1998). FA index for each of the five radial and five ulnar counts was calculated as the absolute value of the difference between the R and L fingers, designated as (|R–L|), according to Jantz and Webb, (1980). The index of asymmetry for ridge counts was examined using the measures of Jantz (1975) that describe the variation in the ridge counts between homologous fingers:

$$\sqrt{A^2} = \sqrt{\sum\nolimits_{i=1}^{5} (R_i - L_i)^2}$$

where $(R_i - L_i)$ is the difference between ridge counts on the corresponding R and L hands' *i*th fingers.

According to the definition of Holt (1960), modified by Jantz (1975), the index of diversity that quantifies the differences between non-homologous fingers was calculated as follows:

$$s/\sqrt{5} = \sqrt{\frac{\sum_{i=1}^{5} q_i^2 - \frac{Q^2}{5}}{5}}$$

where q_i is the sum of corresponding counts of the *i*th pair of homologous fingers, and Q is an individual's total ridge count (TRC) (sum of the higher of the ulnar and radial ridge counts over all 10 fingers).

Population comparisons

The finger ridge count, diversity, and asymmetry index values obtained in this study were compared with those for an Amerindian Aymara ethnic group from Chile (Dittmar 1998) and several populations from different regions of the world organized by geographical origin: European, Western Asian, Indian, Polynesian, and African groups. This grouping and the selected populations are somewhat similar to the grouping and the populations in time in Dittmar (1998). The populations were as follows: (**a**) European or European ancestry: southern (1) and central (2) Sardinian and central Italian (3) (Vona and Porcell, 1983), east European Jews (first generation of Israeli-born descendants of east European immigrant parents) (4) (Kobyliansky and Micle, 1989), Belgian (5) (Leguebe and Vrydagh-Laoureux, 1978), Bulgarian (6) (Karev, 1990), Tennesseans or people from adjacent states (Scottish, Irish and English descent) (7) (Jantz, 1975), people from southeastern England (8) (Jantz, 1975) and southwestern Ohio (9) (Roche et al., 1979); (**b**) Africans or people of African origin; southern USA (10) (Jantz, 1975), Dogon (Mali) (11) (Jantz, 1975), Efe pygmies (Democratic Republic of Congo) (12) (Jantz, 1975), Bedik people in Bassari country (Senegal) (13) (Jantz, 1975); (**c**) Western Asians; Jewish migrants from Middle Eastern countries (Iraq, Syria, Iran) (14) (Kobyliansky and Micle, 1987), Yemenite Jews (Israel) (15) (Micle and Kobyliansky, 1987), Moroccan Jews (Israel) (16) (Kobyliansky and Micle, 1988), Muzeina Bedouins (17) (south Sinai Peninsula, Egypt) (Kobyliansky et al., 1986); and (**d**) Polynesians/people from Easter Island (18) (Jantz, 1975).

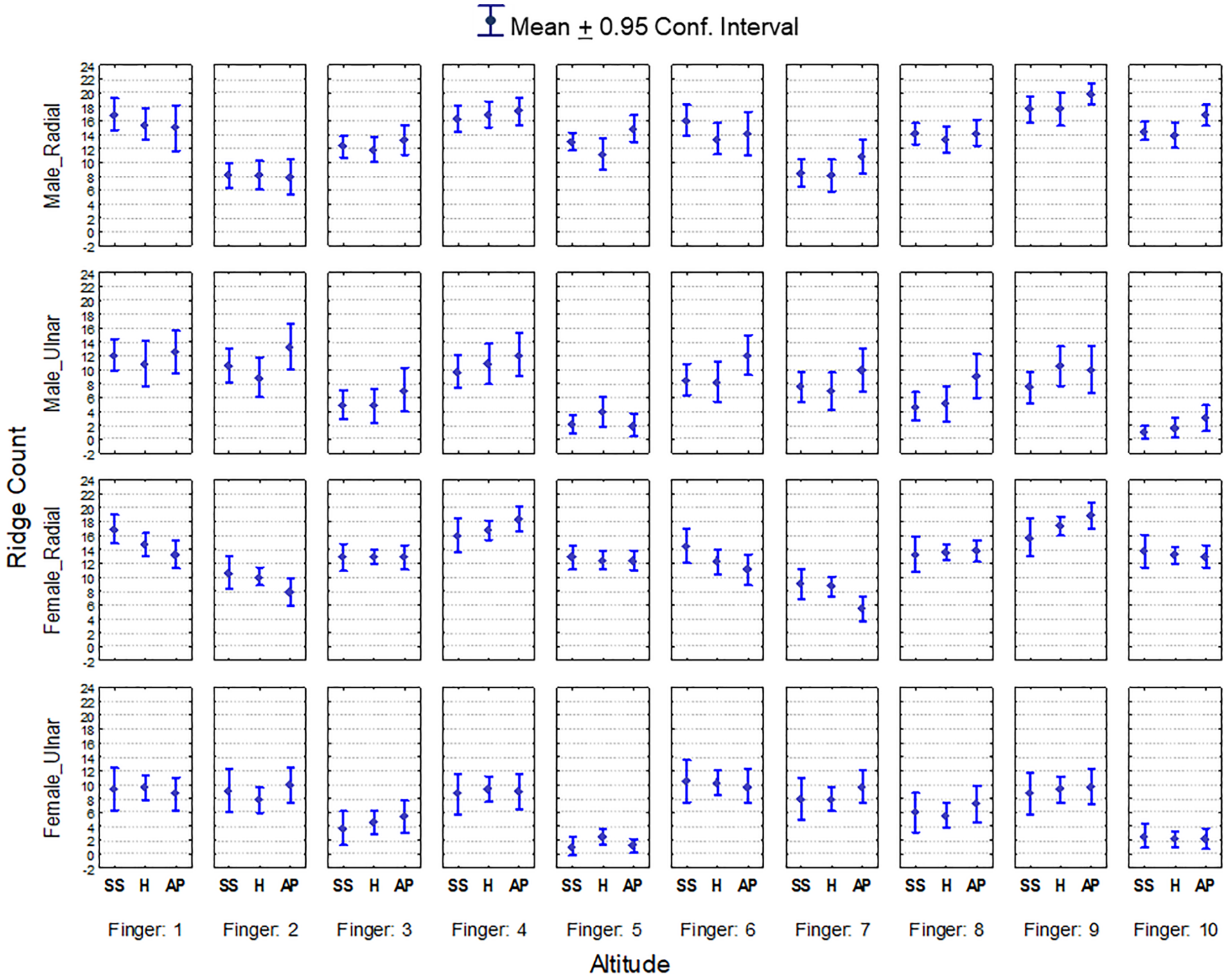

Fig. 1. Mean (± 95% confidence interval) of ulnar and radial ridge count by finger, sex, and locality. SS: San Salvador de Jujuy; H: Humahuaca; AP: Abra Pampa.

Statistical procedures

Ulnar and radial ridge counts of each finger – total ridge count (TRC), the sum of bilateral ulnar ridge counts (URC) and the sum of bilateral radial ridge counts (RRC) were calculated and means and standard deviations were determined for each sex separately. Because most variables used did not follow a normal distribution, the analyses were performed using non-parametric tests, Kruskal–Wallis's tests for comparisons between populations, and Mann–Whitney's tests for comparisons between sexes. Regarding the comparison of related samples, Wilcoxon's tests were used to compare the radial and ulnar areas, and Friedman's tests were used to compare the different variables between fingers.

The median, mean, and standard error of the difference between the R and L sides and the standardized skew and kurtosis of frequency distribution of the R and L sides were calculated to detect the asymmetry pattern. A significance test for differences in FA was conducted (ANOVA).

Spearman's “rho” were used to correlate TRC, diversity ($s/\sqrt{5}$), and asymmetry ($\sqrt{A^2}$) values by sex.

The significance level was fixed at 95% in all cases. Principal components analysis (PCA) was used to explore the relationship between diversity, asymmetry, sex, and populations. Three statistical programs, SPSS 24, Statistica 12, and Statgraphics Centurion XVII, were used for all these analyses.

Results

Counts of radial and ulnar ridges by finger

Fig. 1 shows the 95% confidence intervals of the mean count of radial and ulnar ridges by finger, sex, and locality. From the 40 comparisons made using the Kruskal–Wallis's K test, statistically significant differences between localities were only found for some

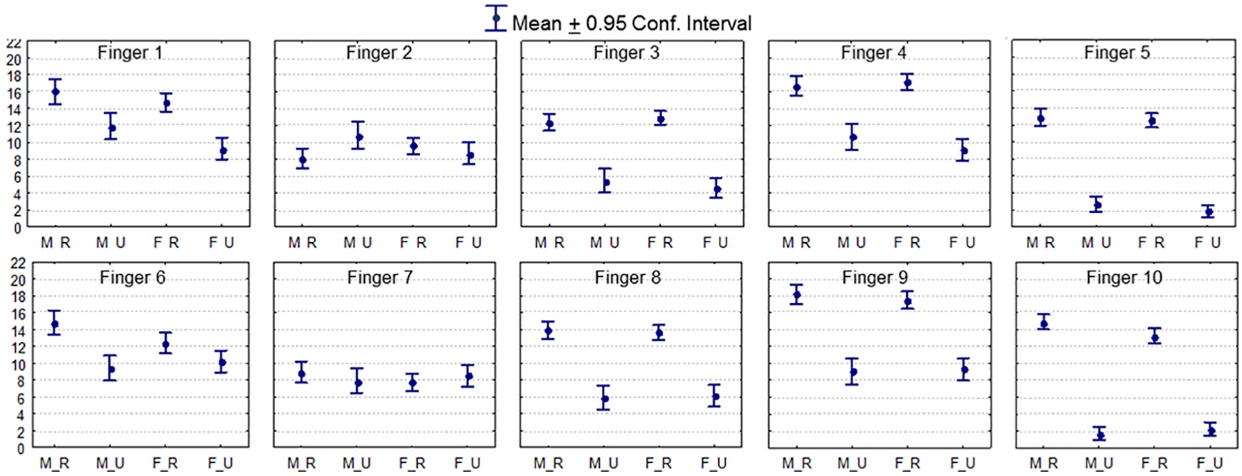

Fig. 2. Mean (± 95% confidence interval) of ulnar and radial ridge count by sex and finger. M: male; F: female; R: radial; U: ulnar.

fingers in terms of radial counts. In fact, statistically significant differences were found in radial counts for little fingers in males (R: $p = 0.007$; L: $p = 0.033$), with higher radial counts in the Abra Pampa sample and lower radial counts in the San Salvador sample. Statistically significant differences were found in radial counts in females for R thumbs ($p = 0.038$) and L index fingers ($p = 0.022$); in this case, the Abra Pampa sample showed the lowest radial counts and the San Salvador sample showed the highest. Nevertheless, the value of Bonferroni's correction was 0.005 that confirmed lack of significance. No statistically significant differences between localities were found in terms of ulnar counts; the three samples showed very similar ridge count means (by finger, side, and sex) (Fig. 1).

As practically no significant difference existed between samples, data were pooled, and ridge counts were compared between fingers and sexes. Fig. 2 shows means and 95% confidence intervals for radial and ulnar counts in males and females by finger. Ridge counts on radial and ulnar sides were positively and significantly correlated for all fingers ($p < 0.05$); individuals with higher ulnar counts also had higher radial counts. A Wilcoxon's test was used to compare radial and ulnar counts in each sex. The radial count was significantly higher than the ulnar count for both sexes and for all fingers, except the index fingers (Fig. 2). A Mann–Whitney's U test was used to compare radial and ulnar counts between the sexes. In the 20 comparisons between sexes, statistically significant differences were only found between males and females in the ulnar counts of R thumbs (F1) and the radial counts of L little fingers (F10), and in both cases males had higher counts. However, the value of Bonferroni's correction was 0.005 that confirmed lack of significance. Count values for the remaining fingers were very similar for both sexes (Fig. 2).

The Friedman's test was used to compare ridge counts of the 10 fingers by area (radial and ulnar). On the radial side, ring and index fingers were significantly different from the rest and showed the highest and lowest ridge counts, respectively. On the ulnar side, thumbs showed a significantly higher ridge count and little fingers the lowest (Fig. 2).

Both sexes showed significant differences in summed radial ridges counts (RRC) and summed ulnar ridges counts (URC), with higher values for RRC in the three localities. However, no significant differences were found for any of the counts (RRC and URC) between localities or sexes (Fig. 3). Nevertheless, males from Abra Pampa had the highest ridge counts on the radial and ulnar sides. Females from Abra Pampa also had higher ulnar counts, while females from San Salvador de Jujuy had higher radial counts.

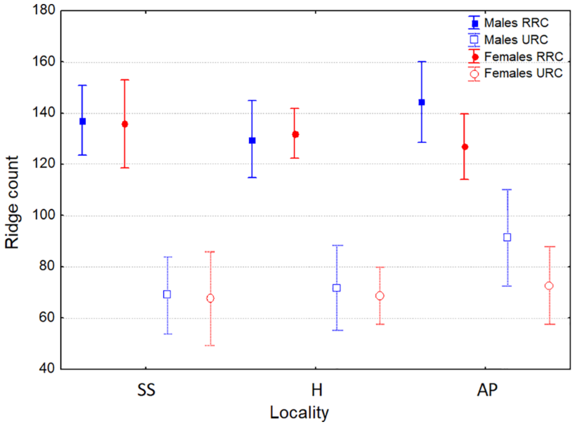

Fig. 3. Mean (± 95% confidence interval) of total ridge count (URC: ulnar ridge count and RRC: radial ridge count) by sex and locality. SS: San Salvador de Jujuy; H: Humahuaca; AP: Abra Pampa.

Table 1
Descriptive statistics of the differences between the right (R) and left (L) sides for the ridge count by locality, sex, side, and finger.

		RADIAL							ULNAR				
		Finger	Count	Mean	Std. Error	Median	Std. Skew	Std. Kurtosis	Mean	Std. Error	Median	Std. Skew	Std. Kurtosis
Male	San Salvador	F1	64	0.859	0.908	0	2.797	3.762	3.578	1.092	0	1.788	0.599
		F2	64	−0.297	0.872	0	−1.132	1.025	3.156	1.018	0	2.441	2.182
		F3	64	−1.875	0.611	−2	−1.220	2.136	0.219	0.409	0	5.250	18.243
		F4	64	−1.391	0.480	−1	−1.413	1.074	2.266	0.899	0	1.858	2.376
		F5	64	−1.531	0.468	−1.5	−0.399	0.053	1.172	0.442	0	10.336	15.242
	Humahuaca	F1	41	2.146	0.933	1	1.831	2.855	2.585	1.299	0	3.643	3.486
		F2	41	0.049	1.084	0	−1.378	1.220	2.024	1.305	0	1.687	0.776
		F3	41	−1.439	0.793	−2	0.208	3.299	−0.317	1.218	0	−0.598	1.963
		F4	41	−0.780	1.123	−2	1.834	3.039	0.293	1.419	0	−0.013	0.649
		F5	41	−2.683	0.890	−1	−3.012	2.222	2.317	0.894	0	5.335	5.115
	Abra Pampa	F1	35	0.771	1.483	0	−1.316	1.989	0.457	1.515	0	0.183	0.545
		F2	35	−2.914	1.474	−1	0.809	1.464	3.400	1.413	2	−0.209	−0.257
		F3	35	−1.057	0.706	−1	−3.804	6.134	−1.971	1.297	0	−1.758	1.079
		F4	35	−2.543	0.561	−1	−4.035	5.431	2.057	1.086	0	3.142	1.475
		F5	35	−1.943	0.542	−1	−2.255	2.010	−1.000	0.672	0	−5.451	6.474
Female	San Salvador	F1	35	2.400	0.896	1	1.857	0.825	−1.114	1.298	0	0.572	2.518
		F2	35	1.714	0.993	1	0.047	2.500	1.257	1.120	0	−0.747	2.699
		F3	35	−0.457	0.820	−1	2.262	1.558	−2.257	1.288	0	−1.448	2.582
		F4	35	0.257	0.922	0	6.958	14.760	−0.086	1.035	0	2.312	2.827
		F5	35	−0.914	0.706	−1	0.479	5.856	−1.514	0.881	0	−0.652	3.819
	Humahuaca	F1	84	2.488	0.709	1	2.416	2.184	−0.762	0.529	0	2.579	9.731
		F2	84	1.476	0.656	0	2.007	1.536	−0.143	0.753	0	−1.766	2.531
		F3	84	−0.702	0.439	−1	2.016	3.372	−1.024	0.641	0	−1.793	4.443
		F4	84	−0.583	0.576	−1	3.458	5.034	0.095	0.841	0	1.296	1.737
		F5	84	−0.643	0.496	−1	2.962	5.150	0.333	0.523	0	2.143	11.821
	Abra Pampa	F1	51	2.196	0.855	1	2.211	1.403	−1.137	1.060	0	−0.635	2.849
		F2	51	2.490	0.869	0	1.603	0.030	0.059	0.816	0	−2.907	5.091
		F3	51	−0.882	0.719	0	−2.317	3.552	−1.804	1.162	0	−1.321	0.643
		F4	51	−0.431	0.490	−1	0.239	1.566	−0.745	0.979	0	−1.618	3.502
		F5	51	−0.588	0.483	0	2.262	4.230	−1.039	0.612	0	−6.404	14.081

Std. – standard.

Fluctuating asymmetry

Table 1 displays the descriptive statistics of ridge count differences between the R and L sides by locality, finger, sex, and side (ulnar and radial). Overall, the results show that the mean of the distribution of the differences between the R and L sides does not differ from zero. In addition, deviations of the frequency distributions of (R–L) from normal in the direction of platykurtosis have not been found. Therefore, DA or antisymmetry patterns have not been found, but FA exists, i.e., small and random deviations from symmetry are present.

The means for the FA indices (|R–L|) are presented in Table 2. In both sexes, the highest values were found in the highland samples (Humahuaca and Abra Pampa), except for the radial area of the middle finger and the ulnar areas of the thumb and little

Table 2
Means and standard error of the means by sex and locality for the fluctuating asymmetry (FA) index (|R–L|) over the five fingers by side.

	Finger	San Salvador				Humahuaca				Abra Pampa			
		Male		Female		Male		Female		Male		Female	
		Mean	Std. Error	Mean	Std. Error	Mean	Std. Error	Mean	Std. Error	Mean	Std. Error	Mean	Std. Error
Radial	F1	4.950	0.669	4.110	0.688	4.390	0.710	4.890	0.537	5.970	1.081	4.350	0.670
	F2	4.700	0.641	4.060	0.767	4.930	0.753	4.400	0.472	6.460	1.093	4.490	0.690
	F3	3.780	0.449	3.600	0.546	3.830	0.561	2.990	0.302	3.000	0.517	3.550	0.529
	F4	2.920	0.354	3.060	0.760	5.070	0.795	3.850	0.398	2.890	0.510	2.590	0.332
	F5	3.060	0.328	2.860	0.532	4.100	0.743	3.190	0.358	2.570	0.459	2.470	0.343
Ulnar	F1	6.140	0.893	4.660	1.041	4.980	1.111	2.950	0.427	6.110	1.097	4.590	0.853
	F2	5.380	0.858	4.110	0.896	5.490	1.027	4.380	0.579	6.660	1.017	3.310	0.668
	F3	1.250	0.379	4.310	1.123	4.460	0.994	3.000	0.561	4.490	1.097	4.940	0.963
	F4	4.140	0.786	3.630	0.827	6.000	1.057	4.950	0.642	3.940	0.920	4.120	0.794
	F5	1.170	0.442	2.490	0.813	2.660	0.870	1.930	0.480	1.630	0.635	1.510	0.592

Std. – standard.

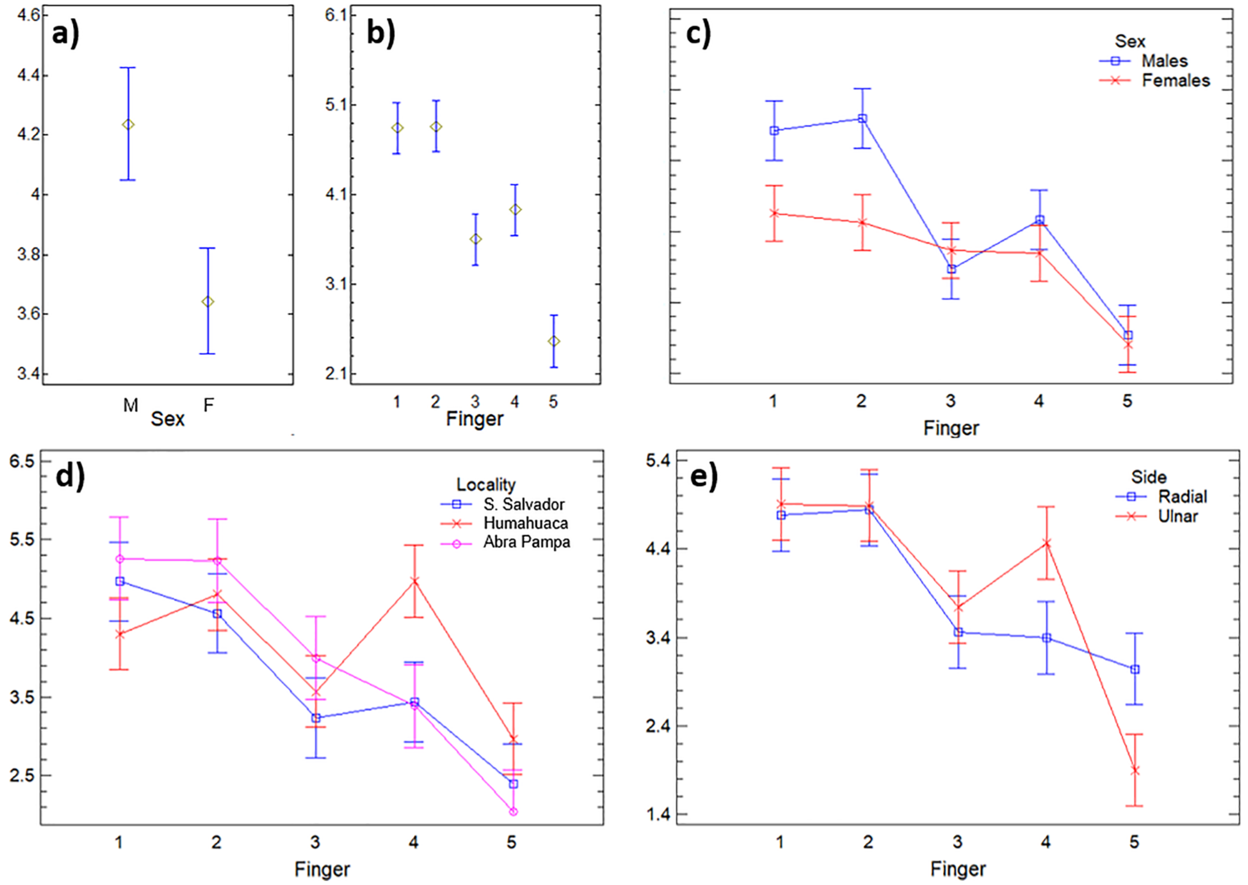

Fig. 4. Mean and 95% least significant difference (LSD) interval of fluctuating asymmetry (FA). (a) FA by sex; M: male, F: female; (b) FA by finger (1…5); (c) 95% LSD intervals and interaction between the variables finger and sex; (d) 95% LSD intervals and interaction between the variables finger and locality; (e) 95% LSD intervals and interaction between the variables finger and side.

finger in females, for whom the values were higher in the lowland samples corresponding to San Salvador.

A multifactorial analysis of the variance was conducted to detect the statistically significant differences in FA by locality, finger, sex, and side (ulnar and radial). The results revealed statistically significant differences in FA by sex ($F = 10.18$, $df = 1$, $p = 0.0014$) and finger ($F = 26.30$, $df = 4$, $p < 0.0001$). However, no significant differences were found by locality or by side (radial and ulnar). When analyzing the interactions between the different factors assessed, it was found that the finger variable showed significant interactions with locality ($F = 2.67$, $df = 8$, $p = 0.0065$), sex ($F = 3.01$, $df = 4$, $p = 0.0171$), and side ($F = 3.66$, $df = 4$, $p = 0.0056$) (Fig. 4). Thus, males presented a significantly higher FA than females (Fig. 4a). The thumbs and index fingers showed a significantly higher FA than the rest of the fingers, while the little finger had significantly lower FA (Fig. 4b). The interaction between fingers and sex showed that the thumbs and index fingers of males had a significantly higher FA than those of females (Fig. 4c). However, the interaction between side (radial and ulnar) and fingers showed significant differences in FA for the ring and little fingers, with higher FA values for the ulnar side in the ring finger and for the radial side in the little finger (Fig. 4e). Finally, the interaction between localities and fingers showed only significant differences in FA for the ring finger, which showed higher values in the Humahuaca samples (Fig. 4d).

Asymmetry and diversity indices

Table 3 shows means and standard deviations by sex for the index of asymmetry ($\sqrt{A^2}$), the index of diversity ($s/\sqrt{5}$), the TRC, the summed URC, and the summed RRC. As can be seen, mean asymmetry and diversity index values are higher in males than in females, indicating more asymmetry and greater heterogeneity among fingers in males, but none of the differences reach statistical significance at the 5% level. The mean ridge counts for TRC, URC, and RRC are higher in males than in females, although no significant differences were found between sexes in any of these counts in the studied sample. These results were compared by sex with those obtained by Dittmar (1998) for the Aymara sample in Chile, and no significant differences were found for males, while females showed significant differences for TRC and RRC that were higher in the Jujuy samples in this study.

Spearman's coefficients of correlation were calculated to examine the relationship between TRC, $s/\sqrt{5}$, and $\sqrt{A^2}$ (Table 4). In both

Table 3
Means and standard deviations (SD) by sex for asymmetry ($\sqrt{A^2}$), diversity ($s/\sqrt{5}$), total ridge count (TRC), summed ulnar ridge count (URC), and summed radial ridge count (RRC).

	Males		Females		Significance of sex difference
	Mean	SD	Mean	SD	
I. Asymmetry	9.01	4.27	8.68	4.11	n.s
I. Diversity	7.01	3.38	6.98	3.26	n.s
TRC	153.61	52.55	145.90	48.10	n.s.
URC	75.51	57.21	69.87	52.37	n.s.
RRC	136.84	50.50	131.28	46.08	n.s.

n.s. – not significant (Mann–Whitney's U test has been used to assess the differences between sexes).

Table 4
Spearman's coefficients of correlation between TRC, diversity ($s/\sqrt{5}$), and asymmetry ($\sqrt{A^2}$) values by sex.

	Males	Females
TRC-s/√5	−0.243*	−0.100
TRC-√A2	−0.332*	−0.163*
√A2-s/√5	0.262*	0.356*

* Significance level: $p < 0.05$.

sexes, correlations between $s/\sqrt{5}$ and $\sqrt{A^2}$ are positive, while correlations of TRC with $s/\sqrt{5}$ and with $\sqrt{A^2}$ are negative, where the correlation of TRC with asymmetry is higher than the correlation of TRC with diversity. All correlations were significant, except the correlation between TRC and diversity in females.

Fig. 5 shows the box-and-whisker plot for asymmetry and diversity indices by locality and sex. In males, the highest values of both indices were found in San Salvador de Jujuy and the lowest were found in Abra Pampa, with statistically significant differences in the diversity index between populations (Kruskal–Wallis's test, $p = 0.030$) but not in the asymmetry index. In females, the highest values for both indices were found in Humahuaca and the lowest were found in San Salvador de Jujuy, although no significant differences were found for either of the two indices. The comparison between sexes of both indices showed no significant differences in any of the population samples studied (Fig. 5).

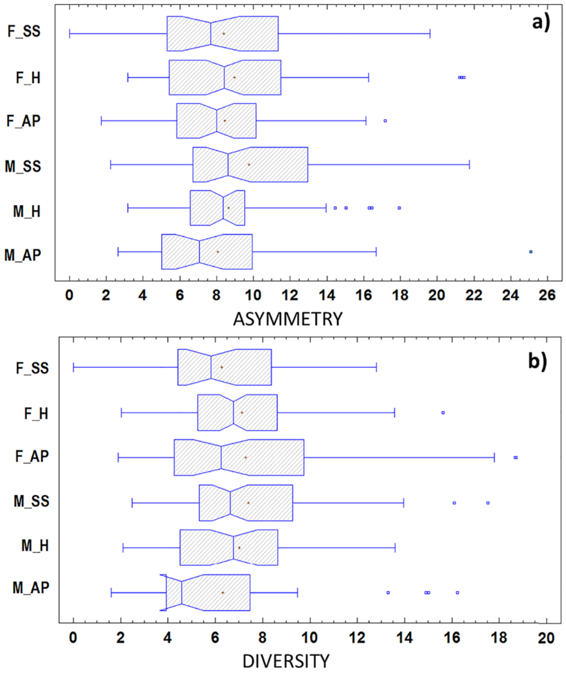

Fig. 5. Box-and-whisker plot with 95% confidence interval for the median by sex (F: female; M: male) and locality (SS: San Salvador de Jujuy; H: Humahuaca; AP: Abra Pampa). (a) Asymmetry; (b) Diversity.

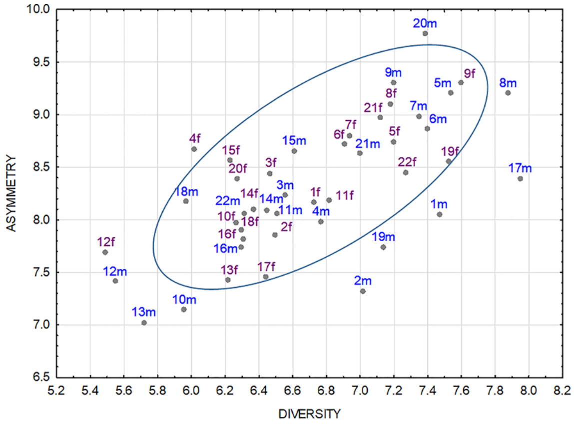

Fig. 6. Bivariate plot showing the relationship between mean values of $s/\sqrt{5}$ and $\sqrt{A^2}$ for each sample. m: male; f: female: (**a**) Europeans or European ancestry; southern (1) and central (2) Sardinian and central Italian (3), east European Jews (first generation of Israeli-born descendants of east European immigrant parents) (4), Belgian (5), Bulgarian (6), Tennesseans or people from adjacent states (Scottish, Irish and English descent) (7), and people from southeastern England (8) and southwestern Ohio (9) (Roche et al., 1979). (**b**) Africans or people of African origin: southern USA (10) (Jantz, 1975), the Dogon (Mali) (11), Efe pygmies (Democratic Republic of Congo) (12), and Bedik people from Bassari country (Senegal) (13). (**c**) Western Asians: Jewish migrants from Middle Eastern countries (Iraq, Syria, Iran) (14), Yemenite Jews (Israel) (15), Moroccan Jews (Israel) (16), and Muzeina Bedouins (17) (south Sinai Peninsula, Egypt). (**d**) Polynesians/people from Easter Island (18), Aymarans (Chile) (19), Argentinians from San Salvador de Jujuy (20), Argentinians from Abra Pampa (21), and Argentinians from Humahuaca (22).

Comparison between populations

Fig. 6 shows the dispersion diagram that relates the asymmetry and diversity indices in the samples of the analyzed populations from Jujuy, the Aymara population, and those populations compiled from other studies cited above (Materials and methods). Of note, females show lower dispersion than males, where the experimental standard error to predict asymmetry as a function of diversity is higher in males than in females (males: $\delta = 0.548926$ females: $\delta = 0.392283$).

Fig. 7 shows the plot of the two PCAs for the asymmetry and diversity indices for males and females in different populations from various geographic areas. Two components were obtained from lineal combinations of the variables diversity-male, diversity-female, asymmetry-male, and asymmetry-female, explaining the 84.64% variability. The first component (69.74% variance) separates the Andean populations from the rest, except some European populations. The second component (14.9% variance) separates the Andean populations located above 2000 m, Aymara, Abra Pampa, and Humahuaca, from those in San Salvador de Jujuy, located at 1200 m.

Discussion

Regardless of the biological significance of the study of the dermatoglyphic diversity from finger to finger and the asymmetry

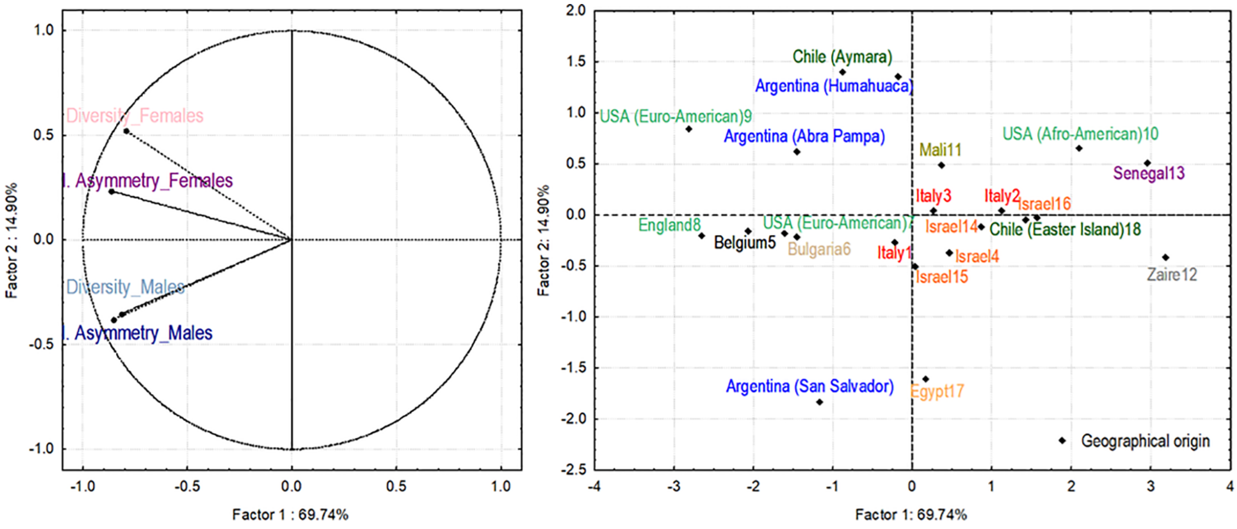

Fig. 7. Principal component analysis (PCA) for the index of asymmetry and diversity, sex, and population samples.

between homologous fingers demonstrated in previous publications (Chakraborty et al., 1982; Dittmar, 1998; Jantz, 1975, Kobyliansky et al., 1986; Kobyliansky and Micle, 1987, 1988; Kusuma et al., 2001; Leguebe and Vrydagh-Laoureux, 1978; Vona and Porcell, 1983), few and very spaced in time references exist on this topic. In particular, very few populations have been analyzed in Latin America so far (de Sá E Benevides and Salzano, 1969; Dittmar, 1998; Parham, 1985; Salzano and de Sá E Benevides, 1974), and the results of this work are the first to refer to Argentine populations residing in high-altitude areas. Like the Aymara population in Chile (Dittmar, 1998), the Abra Pampa and Humahuaca populations are exposed to the hypoxia effect; therefore, their ridge count and asymmetry characteristics may be representative of the original populations of the southern sector of the Andes.

The interest in dermatoglyphs in development biology studies arises from evidence indicating that the expression of dermatoglyphic traits may be drastically altered during the first four months of intrauterine life. Babler (1978, 1979) demonstrated that spontaneously aborted 11–25-week-old fetuses have later ridge maturation, less ridge depth, and a significantly higher arch frequency than a control group comprised of electively aborted fetuses and newborn children. This difference was explained as a prenatal selection against certain fetuses that may have experienced dermatoglyphic development disturbances disclosed by the presence of unusual designs and alterations of the epidermal ridge morphogenesis. These ridge morphogenesis changes due to environmental or genetic factors may take place before 25 weeks of gestation, as at that development stage the epidermal ridge system has an adult morphology that cannot be modified at any other period of ontogeny by any factor. For this reason, together with the fact of the meristic trait, the ridge count is a particularly appropriate feature to assess FA and thus the possible effect of developmental noise.

Regarding the effect of hypoxia on epidermal ridge morphogenesis, no clear information exists about from what time of the prenatal ontogeny the morphophysiologic changes induced by this stressing factor occur, and whether they affect the morphologic development of the ridges. In relation to this uncertainty, the results found in this work simply indicate that no differences in the symmetry of digital ridge count between populations of the same ethnic origin with different stress degrees to the effects of hypoxia occurred, except for the diversity index in males.

The relationship between hypoxia and early fetal development disorders is highly controversial, little studied, and has very few references. Pregnancies at great altitudes are characterized by simultaneity of maternal and fetal hypoxia that lead to a greater risk of intrauterine growth retardation, newborns being small for their gestational age, and increased child mortality (Giussani, 2006). Recent experimental studies of sheep indicate that exposure to high altitude during the very early stages of pregnancy, even in the short term, affects the maternal ovarian steroidogenic function and embryo-fetal growth (Parraguez et al., 2015). However, evidence exists that regardless of the altitude above sea level, oxygen supply to the embryo in the first trimester is tightly controlled; therefore, small variations in the amount of oxygen may interfere in the development of the embryo. Experimental studies on oxygen measurement in mammal embryos may indicate that the embryo would normally be in a state of partial hypoxia during organogenesis (Webster and Abela, 2007), which is essential to control cardiovascular development, very probably controlled by the transcription factor hypoxia-inducible factor (HIF). Periods of more severe hypoxia of different etiologies in the first trimester may cause birth defects, particularly terminal transverse reduction-type limb defects.

Our results show a relative homogeneity of ridge counts between populations and sexes both on the radial and ulnar sides. Indeed, in both cases, ridge count differences are limited to some fingers, where males and the radial side show the highest counts. These significant but isolated differences do not allow any separation between the populations although the populations of Humahuaca and Abra Pampa are different from that of San Salvador de Jujuy, located closer to the sea level, with higher miscegenation and less isolation as it is the capital of the Jujuy Province. However, counts and their distribution by finger, side, and sex are similar to those found by Dittmar (1998) in the Aymara population. In both sexes, the values for digit 1 (thumb) were the highest in terms of ulnar counts, and of the values for digit 4 (ring finger) were highest in terms of for radial counts. The lowest ulnar counts occurred on digit 5 (little finger), and the lowest radial counts occurred on digit 2 (index finger). Likewise, the radial side showed higher values than the ulnar side in both studies, both in individual counts by finger and in global counts (RRC and URC). However, while significant differences were found between these counts in our results in both sexes and for all fingers (except index fingers), females from the Aymara sample did not show significant differences in the left hand. Additionally, in both studies few fingers showed differences by sex for radial and ulnar counts.

Subtle departures from symmetry are most commonly described by different frequency distributions of the difference between the R and L sides. Such frequency distributions usually exhibit different patterns (FA, DA, and antisymmetry, among others) (Van Valen, 1962); all of them concern patterns of variation in a particular trait exhibited by a sample of individuals. Specifically, FA reflects some developmental compromise between two presumably independent but opposing processes—developmental noise and developmental stability.

Traits where one side is consistently larger than the other in the same direction (DA) complicate both the analysis and interpretation of FA variation. For this reason, the presence of DA should be determined in FA studies because DA artificially inflates the values of certain FA indices. In addition, if a trait exhibits DA then some portion of the between-sides variation may have a genetic basis; therefore, the asymmetry pattern may not purely be a product of developmental noise (Palmer and Strobeck, 1992; 2003). Palmer and Strobeck (1992) and Palmer (1994) therefore suggest traits that exhibit significant DA should be excluded from FA analyses. Our research results showed the generalized absence of DA in the frequency distribution of the between-sides differences in the ridge count, thus demonstrating its suitability for assessing FA.

The highland samples (Humahuaca and Abra Pampa) had the highest FA values in our results, although there were no significant differences in FA among the three populations by sex. It is important to point out that given the difficulty of accessing population groups located in the Andean highlands of Jujuy due to the geographical location, the low population density of the area, and the hermeticism of these populations, the sample size obtained did not allow independent replication of the different groups based on geographical altitude. Therefore, more research on this subject is necessary to elucidate the possible effect of hypobaric hypoxia on the development of papillary ridges.

However, there were statistically significant differences in FA by sex, regardless of the geographic location from which the samples originated. These results indicate that males are more affected by developmental noise or have less developmental stability or both. Significant differences in FA were also found between the fingers, where the FA values have a gradient with higher values for the thumbs and index fingers and lower values for the little fingers (thumbs = index > middle = ring fingers); therefore, the fingers also showed different degrees of involvement due to developmental noise or developmental stability or both.

Significant differences were found by sex and finger in the FA results obtained, with a pattern very similar to the one found in the Aymara population. Thus, FA values and the distribution pattern found by finger were similar to those found in the Aymara population by Dittmar (1998). Therefore, on the ulnar and radial sides, especially in males, there tends to be a display of the greatest level of asymmetry on the first and second finger pairs and a display of the lowest level of asymmetry on the fifth finger pairs.

As Jantz (1975) suggests, the relations between the number of ridges by finger are as important as the number of ridges as regards population variations; therefore, the asymmetry (between homologous fingers) and diversity (between non-homologous fingers) indices were assessed. Regarding the asymmetry index, no statistically significant differences were found between populations and sexes. According to Dittmar (1998), the asymmetry index may be used to detect differences in population origins; therefore, it may be deduced that such differences are non-existent in the populations studied with the same ethnic background. The diversity index only showed significant differences in males among the three populations studied. Males from San Salvador showed the highest diversity index and males from Abra Pampa showed the lowest, thus indicating a greater homogeneity in ridge counts for non-homologous fingers in high-altitude populations. Holt (1960) proposed that the diversity index reveals a substantial genetic component due to familial correlations for this index. Inter-population variation among the male samples in this study is explicable in those terms, while the asymmetry index apparently has a high environmental component (Singh, 1970). However, Jantz's (1975) results revealed that levels of inter-finger diversity and asymmetry appear to be patterned along population lines rather than related to any identifiable environmental factor.

Two hypotheses have been suggested to explain the possible genetic mechanisms underlying the variation found between populations as regards TRC, asymmetry and diversity indices (Holt, 1958; Jantz, 1975). Although we know very little about gene action on ridge counts, one of the hypotheses posed by Holt (1958) suggests that for most loci related to TRC heterozygous individuals will show the highest levels asymmetry or inter-fingers diversity. The second hypothesis refers to the genetic control of developmental stability or channeling. Jantz (1975) showed that the groups with greater homogeneity between fingers were or had recently been tribal populations, where environmental stresses might be expected to be greater than those experienced by groups with a long history of civilization. Under such circumstances, it could be considered that the genotypes more capable of tolerating environmental damage may have a selective advantage, resulting in greater developmental stability for such groups. With the present evidence, it is not possible to tell which of these two hypotheses is more defensible, although they are not necessarily mutually exclusive. According to these hypotheses, the samples analyzed from Jujuy and the Aymara population studied by Dittmar (1998) may show the same with reference to heterozygous to homozygous ratio, as no asymmetry value differences between them were found. The significant differences found in the diversity index between the male samples from a higher geographical altitude in Abra Pampa may indicate a substantially different genetic component and not a selection due to some type of environmental stress. Although in our study diversity index differences between localities cannot be attributed to altitude, other authors have found differences in the asymmetry index due to altitude. Parham (1985) found statistically significant differences in the mean asymmetry of palm ridge counts in males but not in females in a study of Quechua Peruvians from the highlands and lowlands. Dipierri et al. (2014) analyzed the association between finger dermatoglyphic patterns and altitude and surname distribution, as well as the biological affinity of the population from Jujuy with other South American natives and admixed populations. The results showed that the distribution of dermatoglyphic patterns of the population of Jujuy belongs to the Andean gene pool and a possible effect of geographic altitude on dermatoglyphic design distributions (arch, radial loop, ulnar loop, and whorl).

Finally, the comparison of the asymmetry and diversity indices between populations confirms the population variation and usefulness of such indicators in establishing biological affinities between populations (Jantz, 1975). The findings in these comparisons are consistent in the sense of clearly grouping the Andean populations of Aymara and in this work, separating them from others geographically and ethnically more distant, except some European populations where nearness may be explained by the influence of the European parental stem in the conformation of these mixed populations (Wang et al., 2008). Group analysis also reveals the differential miscegenation of these populations due to geographic altitude and the consequent cultural and social isolation. Due to their nearness and localization on the Puna grassland and its foothills, these populations kept tight contact and exchanges in the past, reflected by the analysis of principal components that demonstrates that the indigenous genetic identity generated in the past still persists in the present.

The Province of Jujuy in northwest Argentina is an interesting area to evaluate the influence of a diverse and rugged physical environment on the genetic background of the human populations living there. Its population is distributed over an altitudinal gradient varying between 500 and 4000 m. The genetic diversity of the subpopulation from Jujuy located on this altitudinal gradient shows a clear decreasing trend from the higher region (Puna) where Abra Pampa is located to the lower region (valleys) where San Salvador de Jujuy is located (Gómez-Pérez et al., 2011, 2013). The results in this work about dermatoglyphic features (count and asymmetry indices) partially coincide with these references. The microevolutionary process that conditions the genetic and dermatoglyphic characteristics of the people of Jujuy living at different altitudes may be conditioned by the interaction of genetic drift and gene flow. The combined effect of a restricted gene flow with an intense genetic drift fosters the dermatoglyphic and genetic patterns observed in Jujuy Province.

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References

Albert, A.M., Greene, D.L., 1999. Bilateral asymmetry in skeletal growth and maturation as an indicator of environmental stress. Am. J. Phys. Anthropol. 110, 341–349.

Avena, S.A., Via, M., Ziv, E., Pérez-Stable, E., Gignoux, C.R., Dejean, C., Huntsman, S., Torres Mejía, G., Dutil, J., Matta, J.L., Beckman, K., Burchard, E.G., Parolin, M.L., Goicoechea, A., Acreche, N., Boquet, M., Ríos, M.C., Fernández, V., Rey, J., Stern, M.C., Carnese, R.F., Fejerman, L., 2012. Heterogeneity in genetic admixture across different regions of Argentina. PLoS One 7 (4), e34695.

Babler, W.J., 1978. Prenatal selection and dermatoglyphic patterns. Am. J. Phys. Anthropol. 48, 21–28.

Babler, W.J., 1979. Quantitative differences in morphogenesis of human epidermal ridges. In: Wertelecki, W., Plato, C.C. (Eds.), Dermatoglyphics-Fifty Years Later. Alan R. Liss, New York, pp. 199–210.

Bailit, H.L., Workman, P.L., Niswander, J.D., Mac Lean, C.J., 1970. Dental asymmetry as an indicator of genetic and environmental conditions in human populations. Hum. Biol. 42, 626–638.

Barrett, C.K., Guatelli-Steinberg, D., Sciulli, P.W., 2012. Revising dental fluctuating asymmetry in neandertals and modern humans. Am. J. Phys. Anthropol. 149, 193–204.

Beall, C., 2006. Andean, Tibetan, and Ethiopian patterns of adaptation to high-altitude hypoxia. Integ. Comp. Biol. 46, 18–24.

Buchwald, W., Grubska, B., 2012. A complex evaluation of the asymmetry of dermatoglyphs. HOMO – J. Comp. Hum. Biol. 63, 385–395.

Chakraborty, R., Malhotra, K.C., Tateno, Y., 1982. Variations on dermal ridges in nine population groups of Maharashtra, India. III. Asymmetry and interdigital diversity. Am. J. Phys. Anthropol. 58, 53–57.

Cummins, H., Midlo, C., 1961. Finger Prints Palms and Soles: An Introduction to Dermatoglyphics. Dover Publications, New York.

de Bruin, E.I., Graham, J.H., Louwerse, A., Huizink, A.C., 2014. Mild dermatoglyphic deviations in adolescents with autism spectrum disorders and average intellectual abilities as compared to typically developing boys. Autism Res. Treat. 968134https://doi.org/10.1155/2014/968134. Epub 2014 Nov 19.

de Sá E Benevides, F.R., Salzano, F.M., 1969. Fingerprint of whites and negroes from Southern Brazil. Am. J. Phys. Anthropol. 31, 59–63.

Dipierri, J.E., Alfaro, E., Martínez-Marignac, V.L., Bailliet, G., Bravi, C.M., Cejas, S., Bianchi, N.O., 1998. Paternal directional mating in two Amerindian subpopulations located at different altitudes in northwestern Argentina. Hum. Biol. 70, 1001–1010.

Dipierri, J.E., Alfaro, E., Peña, J.A., Constans, J., Dugoujon, J.M., 2000. GM, KM immunoglobulin allotypes and other serum Genetic markers (HP, GC, PI and TF) among South American populations living at different altitudes (Jujuy Province, Argentina): Admixture estimates. Hum. Biol. 72, 305–319.

Dipierri, J.E., Gutiérrez-Redomero, E., Alonso-Rodríguez, C., Alfaro, E., Demarchi, D., Rivaldería, N., 2014. Surnames, geographic altitude, and digital dermatoglyphics in a male population from the province of Jujuy (Argentina). HOMO – J. Comp. Hum. Biol. 65, 256–266.

Dittmar, M., 1998. Finger ridge-count asymmetry and diversity in Andean Indians and interpopulation comparisons. Am. J. Phys. Anthropol. 105, 377–393.

Giussani, D.A., 2006. Hypoxia, fetal growth and developmental origins of health and disease. In: Wintour-Coghlan, E.M., Owens, J.A. (Eds.), Early Life Origins of Health and Disease. Springer Science + Business Media, New York, pp. 219–224.

Gómez-Pérez, L., Alfonso-Sánchez, M.A., Dipierri, J.E., Alfaro, E., García-Obregón, S., De Pancorbo, M.M., Bailliet, G., Peña, J.A., 2011. Microevolutionary processes due to landscape features in the province of Jujuy (Argentina). Am. J. Hum. Biol. 23, 177–184.

Gómez-Pérez, L., Alfonso-Sánchez, M.A., Dipierri, J.E., Sánchez, D., Espinosa, I., De Pancorbo, M.M., Peña, J.A., 2013. Young Alu insertions within the MHC class I region in Native American populations: insights into the origin of the MHC-Alu repeats. Am. J. Hum. Biol. 25, 359–365.

Graham, J.H., Raz, S., Hel-Or, H., Nevo, E., 2010. Fluctuating asymmetry: Methods, theory, and applications. Symmetry 2, 466–540.

Holt, S.B., 1952. Genetics of dermal ridges: bilateral asymmetry in finger ridge-counts. Ann. Eugen. 17, 211–231.

Holt, S.B., 1958. Genetics of dermal ridges: The relation between total ridge-count and the variability of counts from finger to finger. Ann. Hum. Genet. 22, 323–339.

Holt, S.B., 1960. Genetics of dermal ridges: familial correlations for, a measurement of the diversity of ridge-counts from finger to finger. Ann. Hum. Genet. 24, 253–269.

Holt, S.B., 1968. The Genetics of Dermal Ridges. Charles C. Thomas, Springfield, IL.

Jantz, R.L., 1975. Population variation in asymmetry and diversity from finger to finger for digital ridge-counts. Am. J. Phys. Anthropol. 42, 215–224.

Jantz, R.L., 1978. Sex and lateral asymmetry of the finger ridge-count. Ann. Hum. Biol. 5, 285–286.

Jantz, R.L., Webb, R.S., 1980. Dermatoglyphic asymmetry as a measure of canalization. Ann. Hum. Biol. 7, 489–493.

Karev, G.B., 1990. Asymmetry and intraindividual diversity in digital dermatoglyphics of Bulgarians. Am. J. Hum. Biol. 2, 63–73.

Karmakar, B., Malkin, I., Kobyliansky, E., 2013. Inheritance of dermatoglyphic asymmetry and diversity traits in twins based on factor: variance decomposition analysis. Coll. Antropol. 37, 537–543.

Kobyliansky, E., Micle, S., 1989. Dermatoglyphic sexual dimorphism in East European Jews. Bull. Mém. Soc. Anthrop. Paris 1, 13–36.

Kobyliansky, E., Micle, S., 1987. Dermatoglyphic sexual dimorphism in Middle Eastern Jews. Bull. Mém. Soc. Anthrop. Paris 14, 271–290.

Kobyliansky, E., Micle, S., 1988. Dermatoglyphic sexual dimorphism in North African Jews. Int. J. Anthropol. 3, 77–91.

Kobyliansky, E., Micle, S., Hershkovitz, I., Arensburg, B., 1986. The dermatoglyphic characteristics of two isolated Bedouin groups from south Sinai. Int. J. Anthropol. 1, 59–74.

Kusuma, Y.S., Babu, B.V., Naidu, J.M., 2001. Asymmetry of finger ridge counts among four tribal populations of Andhra Pradesh, India. HOMO – J. Comp. Hum. Biol. 52, 110–116.

Leguebe, A., Vrydagh-Laoureux, S., 1978. Diversity and asymmetry of finger ridge-counts in a sample of the Belgian population. Bull. Soc. Roy. Belge Anthrop. Préhist. 89, 135–144.

Mather, K., 1953. Genetical control of stability in development. Heredity 7, 297–336.

Micle, S., Kobyliansky, E., 1987. Dermatoglyphic sexual dimorphism in Yemenite Jews. Bull. Mém. Soc. Anthrop. Paris 14, 95–114.

Milnea, B.J., Belsky, J., Poultona, R., Murray Thomson, W., Caspid, A., Kieser, J., 2003. Fluctuating asymmetry and physical health among young adults. Evol. Hum. Behav. 24, 53–63.

Mukherjee, A., 1990. Inbreeding effects on bilateral asymmetry of dermatoglyphic patterns. Am. J. Phys. Anthropol. 81, 77–89.

Palmer, A.R., 1994. Fluctuating asymmetry analyses: a primer. In: Markow, T.A. (Ed.), Developmental Instability: Its Origins and Evolutionary Implications. Kluwer, Dordrecht, Netherlands, pp. 335–364.

Palmer, A.R., 1996. Waltzing with asymmetry. BioScience 46, 518–532.

Palmer, A.R., Strobeck, C., 1992. Fluctuating asymmetry as a measure of developmental stability: implications of non-normal distributions and power of statistical tests. Acta Zool. Fennica 191, 57–72.

Palmer, A.R., Strobeck, C., 2003. CH 17. Fluctuating asymmetry analyses revisited. In: Polak, M. (Ed.), Developmental Instability: Causes and Consequences. Oxford University Press, Oxford, pp. 279–319.

Parham, K.R., 1985. Developmental Implications of Palmar Dermatoglyphics among Highland and Lowland Quechua. PhD dissertation. University of Tennessee, Knoxville.

Parraguez, V.H., Mamani, S., Cofré, E., Castellaro, G., Urquieta, B., De Los Reyes, M., Astiz, S., Gonzalez-Bulnes, A., 2015. Disturbances in maternal steroidogenesis and appearance of intrauterine growth retardation at high-altitude environments are established from early pregnancy. Effects of treatment with antioxidant vitamins. PLoS One 10 (11), e0140902.

Penrose, L.S., 1968. Memorandum on dermatoglyphic nomenclature. Birth Defects Orig. Artic. Ser. 6, 1–13.

Roche, A.F., Siervogel, R.M., Roche, E.M., 1979. Digital dermatoglyphics in a white population from southwestern Ohio. In: Wertelecki, W., Plato, C.C. (Eds.), Dermatoglyphics-Fifty Years Later. Alan R. Liss, New York, pp. 389–409.

Salzano, F.M., de Sa E Benevides, F.F., 1974. Fingerprint quantitative variation and asymmetry in Brazilian Whites and Blacks. Am. J. Phys. Anthropol. 40, 325–328.

Schlager, S., Rüdell, A., 2015. Analysis of the human osseous nasal shape – population differences and sexual dimorphism. Am. J. Phys. Anthropol. 157, 571–581.

Singh, S., 1970. Inheritance of asymmetry in finger ridge counts. Hum. Heredity 20, 403–408.

Tomaszewska, A., Kwiatkowska, B., Jankauskas, R., 2015. Is the area of the orbital opening in humans related to climate? Am. J. Hum. Biol. 27, 845–850.

Van Dongen, S., 2006. Fluctuating asymmetry and developmental instability in evolutionary biology: past, present and future. J. Evol. Biol. 19, 1727–1743.

Van Dongen, S., Gangestad, S.W., 2011. Human fluctuating asymmetry in relation to health and quality: a meta-analysis. Evol. Hum. Behav. 32, 380–398.

Van Valen, L., 1962. A study of fluctuating asymmetry. Evolution 16, 125–142.

Vilahur, N., Allin, M.P., Walshe, M., Nosarti, C., Rifkin, L., Murray, R.M., Rosa, A., 2012. Ectodermal markers of early developmental impairment in very preterm individuals. Psychiatry Res. 200, 715–718.

Vona, G., Porcell, P., 1983. Asymmetry and interfinger variability of ridge counts in three samples of Italian population. Coll. Antropol. 7, 21–27.

Wang, S., Ray, N., Rojas, W., Parra, M.V., Bedoya, G., Gallo, C., Poletti, G., Mazzotti, G., Hill, K., Hurtado, A.M., Camrena, B., Nicolini, H., Klitz, W., Barrantes, R., Molina, J.A., Freimer, N.B., Bortolini, M.C., Salzano, F.M., Petzl-Erler, M.L., Tsuneto, L.T., Dipierri, J.E., Alfaro, E.L., Bailliet, G., Bianchi, N.O., Llop, E., Rothhammer, F., Excoffier, L., Ruiz-Linares, A., 2008. Geographic patterns of genome admixture in latin american mestizos. PLoS Genet. 4 (3), e1000037.

Webster, W.S., Abela, D., 2007. The effect of hypoxia in development. Birth Defects Res. C. Embryo Today 81, 215–228.