Available online at www.sciencedirect.com

SCIENCE DIRECT®

C. R. Palevol 3 (2004) 403–409

COMPTES RENDUS

PALEVOL

Human Palaeontology and Prehistory

Amerindians: testing the hypothesis about their homogeneity

Marina L. Sardi [a,b,*], Fernando Ramírez Rozzi [a],
Silvia L. Dahinten [c], Héctor M. Pucciarelli [b]

[a] *UPR 2147, « Dynamique de l'évolution humaine », CNRS, 44, rue de l'Amiral-Mouchez, 75014 Paris, France*
[b] *Departamento Científico de Antropología, Facultad de Ciencias Naturales y Museo, Universidad Nacional de la Plata, Paseo del Bosque S/N, 1900, La Plata, Argentina*
[c] *Centro Nacional Patagónico. CONICET. Boulevard Brown S/N, 9120, Puerto Madryn, Argentina*

Received 20 October 2003; accepted after revision 19 April 2004

Presented by Yves Coppens

Abstract

One of the postulates of the most accepted models about the peopling of the Americas proposes that Amerindians constitute a homogeneous population. The aim of the present study is to assess the homogeneity of the craniofacial morphology of South American Amerindians in a worldwide context. Variance of each geographical region and F_{ST} values among local populations were obtained. Results indicate that the southern Amerindians present a high level of morphologic variation, even when geographically closer populations are compared. The origin of Amerindians as well as micro evolutionary processes, which would explain the high variability, is discussed. ***To cite this article: M.L. Sardi et al., C. R. Palevol 3 (2004).***

Résumé

Amérindiens : évaluation de l'hypothèse sur leur homogénéité. Les modèles les plus acceptés pour expliquer le peuplement des Amériques supposent que les Amérindiens constituent une population homogène. L'objectif de cette étude est de tester l'homogénéité de la morphologie crâniofaciale des groupes Amérindiens de l'Amérique du Sud par rapport à un échantillon mondial. Nous avons calculé la variance pour chaque région géographique, ainsi que les F_{ST} entre populations locales d'une même région. Les résultats suggèrent que les Amérindiens sud-américains présentent une variation élevée. L'origine des Amérindiens et les processus micro-évolutifs qui pourraient se trouver à la base de la variabilité amérindienne sont discutés. ***Pour citer cet article : M.L. Sardi et al., C. R. Palevol 3 (2004).***

Keywords: Amerindians; Craniofacial morphology; Variation

Mots clés : Amérindiens ; Morphologie crâniofaciale ; Variation

---

* Corresponding author.
E-mail address: msardi@fcnym.unlp.edu.ar (M.L. Sardi).

doi:10.1016/j.crpv.2004.04.001

Version française abrégée

Les modèles de Trois (TMM) [14] et Quatre (QMM) migrations [25,26] qui expliquent le peuplement des Amériques suggèrent que les Amérindiens résultent d'une seule vague migratoire provenant de l'Asie du Nord-Est et qu'ils sont donc morphologiquement homogènes. L'objectif de cette étude est de tester l'homogénéité de la morphologie crâniofaciale des Amérindiens dans le cadre de la variation mondiale.

La variation morphologique a été évaluée par un « modèle d'évolution neutre » [31,32]. D'après ce modèle [30], la variance régionale peut être évaluée en prenant, soit les régions géographiques (ARG), soit les populations locales de chaque région (APL) comme unités d'analyse. Dans ARG, la variation d'une région est déduite par sa variance observée. Dans APL, le F_{ST} indique la quantité de variation d'une région qui est due aux différences entre populations locales. Sept régions géographiques ont été incluses dans ARG (Europe, Asie, Australasie, Polynésie, Afrique sud-saharienne, Amériques et Patagonie) (Tableau 1) et trois populations locales de chaque région ont été utilisées pour réaliser un APL. Trois autres populations amérindiennes ont été ajoutées aux précédentes pour effectuer un APL seulement entre des Amérindiens.

Quarante-trois mesures de Howells [18] (Tableau 2), après standardisation Q [5], ont été utilisées. Les matrices de variance-covariance ont été calculées avec une héritabilité de 0,55 [7].

Dans ARG, le F_{ST} non-biais est de 0,1492 (erreur standard = 0,0015). Les régions de Patagonie et d'Afrique sud-saharienne montrent les variances les plus élevées (Tableau 3), ce qui indique que la variation dans ces régions est plus élevée que celles des autres régions. Dans APL, le F_{ST} pour les populations de Patagonie occupe la troisième position indiquant une variation plus élevée que celle d'autres populations largement dispersées (Tableau 3). Les F_{ST} pour les autres régions sont très semblables à ceux obtenus par Relethford [30], dont la différenciation est associée à la distribution géographique. L'APL fait avec les échantillons d'Amérique du Sud montre une distribution de F_{ST} avec une moyenne de 0,1573, un F_{ST} minimum de 0,0890 (pour les populations de Patagonie) et un F_{ST} maximum de 0,2180. Bien que les populations de Patagonie aient une variation élevée par rapport aux populations d'autres continents (Tableau 3), la variation entre elles correspond à la plus faible parmi les Amérindiens.

Les résultats indiquent que les Amérindiens ne présentent pas une morphologie crâniofaciale homogène, comme le veulent les modèles plus acceptés. La variation élevée des Amérindiens peut être due à : (a) un peuplement plus ancien, (b) plusieurs vagues migratoires, (c) des populations à grand nombre d'individus, (d) un taux élevé de croissance démographique, (e) un degré élevé d'isolation et (f) des facteurs environnementaux. Le point (a) étant proposé par quelques auteurs [11,15,16,27,33] semble probable, mais l'évidence archéologique d'occupation est faible [8]. L'option (b) est écartée, si on considère la variation en Asie, car la diversité observée en Sibérie [20] ne peut pas expliquer la variation élevée des Amérindiens. Des études en génétique ont trouvé des rapports entre les Amérindiens et les Asiatiques [6,23], mais la localisation géographique du groupe ancêtre reste douteuse [11,22,23,38]. Par ailleurs, la variation élevée peut résulter du fait que certains groupes amérindiens soient des descendants des Paléoaméricains (premiers groupes à peupler l'Amérique à la fin du Pléistocène) [13], ce qui n'est pas considéré par le modèle de Quatre Migrations [25,26]. Les points (c) et (d) devraient être écartés, car la taille des populations des chasseurs-cueilleurs augmente rarement et encore moins dans un environnement instable [33,37]. Les points (e) et (f) s'appuient sur l'évidence archéologique qui suggère que les Amériques étaient largement peuplées vers 13000 AP [8]. L'isolement des groupes dû à un environnement aride qui aurait réduit la mobilité aurait favorisé la dérive génétique en augmentant donc la variation (point (e)). Mais l'adaptation mise en évidence par le registre archéologique n'est pas une preuve de variation morphologique (point (f)). Mais, bien que l'influence de l'environnement ne puisse pas être négligée, il reste difficile de comprendre pourquoi la pression de l'environnement aurait été plus importante en Amérique que dans le reste des continents.

En conclusion, la variation des Amérindiens du Sud est très élevée. Elle peut être expliquée par : (1) une grande dispersion des populations, avec un faible nombre d'individus, dans un environnement instable et fragmenté ; (2) la présence, parmi ceux-ci, des descendants directs des premiers habitants, les Paléoaméricains ; (3) l'existence de plusieurs vagues migratoires vers l'Amérique en provenant de l'Asie, mais d'autres régions géographiques ; et (4) un peuplement plus ancien que 13000 ans. La contribution faite dans cette étude, du point de vue de la morphologie crâniofaciale chez les Amérindiens du Sud, ne permet pas de résoudre le débat sur leur évolution, mais il oblige à reconsidérer les modèles plus acceptés.

1. Introduction

Among the theories concerning the peopling of the Americas, the 'Three' [14] and the 'Four' [25,26] migration models (TMM and FMM, respectively) are the mostly accepted. In both models, the term 'Amerindians' refers to all American Indians, with the exception of Na-Dene, Eskimos and, according to the FMM, Paleoamericans – the most ancient inhabitants of Americas. They propose that Amerindians are descendants of a unique migratory wave coming from the North-East of Asia, so they would constitute a homogeneous population. Nevertheless, some genetic [3,9,28,35], linguistic [27] and morphologic [2,17,21,34] studies suggest that Amerindians do not behave as predicted by these models. The aim of this study is to assess the homogeneity of Amerindian craniofacial morphology in a worldwide context. According to the TMM and the FMM, it is expected to find low levels of morphologic variation among southern Amerindians.

2. Materials and methods

Assessment of morphologic variation was based on a "neutral model bound" approach [31,32]. According with Relethford [30], there are two ways to assess the regional variance: the geographic regions or the local populations of each region can be taken as the unit of analysis (*among-regions* and *among-local populations* analyses, respectively). In the first case, a unique F_{ST} for the entire comparative context is obtained which measures the proportion of the total variation that is due to differences among the units analysed (regions). The variation is deduced from the observed variances. In the second case, a F_{ST} for each region is obtained. It has the advantage over the first case that it allows to deduce which part of the entire variation in a geographic region is due to the among-local populations differentiation.

For the *among-regions* analysis, seven world regions (South-Saharan Africa, Europe, Australasia, Asia, Polynesia, Americas, and Patagonia) each one represented by three local populations were compared. For the first six regions, data come from the Howells' database and the selected populations (Table 1) are those used by Relethford [30]. For the seventh one, Patagonia, measurements were obtained by one of us (MLS). Patagonia seems to have been occupied by a unique migratory wave. Even when the contact with northern groups has been demonstrated [12], an intense gene flow was improbable and moreover, this region never underwent an important demographic growth [1]. Thus, a low variation is expected among Patagonians. They are represented by two northern samples: Chubut River Valley (CH, n = 99) and Rio Negro River Valley (RN, n = 72), and a southern one: Tierra del Fuego (TF, n = 45) (Fig. 1). The *among-local populations* analysis was made with the samples included in the *among-regions* analysis. A second *among-local populations* analysis was carried out with Peru, CH, RN and TF and with three additional samples (Fig. 1): the Bolivian sample (BO, n = 19) of 'aymará-quechua' origin, localised in the Andean highlands; the hunter-gatherers of the Paraná River Delta (PD, n = 38), with an antiquity estimated by archaeological associations around 2000 years BP [39]; and the western Pampas sample (WP, n = 37) which represents a Mapuche population that settled in the Pampas after migrate from the southern Andean region [4]. Data for these three samples were collected by one of us (MLS).

Forty-three craniometrical linear Howells' variables [18] were used in the study (Table 2). They were transformed in dimensionless vectors through the Q-standardisation [5] to remove size, whose variation among Amerindians is attributed to environmental factors [17,21,34]. Following previous studies [31,32]

Table 1
List of compared samples derived from Howells' database.
Échantillons comparés, dérivés de la base de données de Howells

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

Fig. 1. Geographical localization of South Amerindian populations.
Fig. 1. Localisation géographique des populations sud-amérindiennes.

additive genetic variance-covariance matrixes, from the phenotypic ones, were calculated with a heritability of 0.55. This value was estimated by Devor [7] and represents an average proportion for metric characters. In the *among-regions* analysis, the regional variation was calculated through observed variances; in the *among-local populations* analysis, the regional variation is represented by the F_{ST} values.

3. Results

In the *among-regions* analysis, an unbiased F_{ST} of 0.1492 (standard error = 0.0015) and a mean variance of 0.819 between all the regions were obtained. Patagonia and South Saharan Africa show the greatest observed variances (Table 3). In the *among-local populations* analysis, the F_{ST} values are very similar to those obtained by Relethford [30] who found a significant association of the among-populations differentiation and the geographic distances. In this context, Patagonia occupies the third position after Polynesia and the Americas showing a higher variation than larger regions (Table 3).

F_{ST} values were obtained with BO, WP, PD, CH, RN, TF and the Howells' Peru samples. Each combination of three South American samples produced thirty-five normally distributed F_{ST} values. The minimum value is that of Patagonia (0.0890), the maximum 0.2180 represents the comparison of WP, PD and Peru. The mean of the distribution is 0.1573 with a standard deviation of 0.0323. F_{ST} values for the geographically closest groups are: 0.135 (CH, RN, PD), 0.162 (CH, RN, WP), 0.179 (RN, PD, WP) and 0.203 (CH, PD, WP).

4. Discussion

Results indicate that the South Amerindians are far from being a homogeneous group in cranial morphologic terms (Table 3). Gene flow with Europeans should be discarded due to the absence of morphologic affinities between Europeans and these Amerindian groups [34]. The low variation among Patagonians regarding other Amerindians supports their unique origin inside America. However, it is worth to know that these same groups from Patagonia show the first and the third highest variations in a worldwide context (Table 3). The high variation in Amerindians can be associated to: (a) a greater antiquity of the peopling, (b) several waves of migration, (c) greater effective population size, (d) greater rate of population growth, (e) greater degree of isolation, and (f) adaptative factors.

The option a), a peopling before 15000 years ago, has been suggested by many authors [15,16,27,33]. This option seems probable even when archaeological sites older than 13000 BP [16] are not accepted without doubts [8].

Option b) is difficult to accept in the context of the TMM and FMM models that suggest that Amerindian

Table 2
List of Howells' craniometric measurements.
Mensurations crâniométriques de Howells

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

Table 3
Estimation of variance on the seven geographic regions.
Estimation de la variance dans sept régions géographiques

Unit of analysis	*Regions*	*Local populations*	
Region	**Observed variance**	F_{ST}	**Mean variance**
South-Saharan Africa	0.87	0.0825	0.938
Europe	0.824	0.0549	0.925
Asia	0.816	0.0371	0.961
Australasia	0.742	0.0686	0.924
Polynesia	0.793	0.1205	0.836
Americas	0.789	0.1005	0.893
Patagonia	0.901	0.0889	0.926

characteristics must reflect the northeastern Asiatic ones. However, in Siberia or Beringia a high variation is not reflected before Holocene times. Kozintsev et al. [20] mentioned that Baikalians, about 8000 years BP, had extremely flat faces and the later inhabitants were less "mongoloids" due to gene flow with European populations. But for both the TMM and FMM the arrival of Amerindians was at the Terminal Pleistocene, so the Siberian holocenic diversity does not explain, therefore, the Amerindian one.

If another than an eastern Asiatic origin is considered, the morphologic diversity is easier to be explained. Genetic studies support the Asiatic origin of American Indians [6,23,24] without accord about the geographic localization of the ancestor [11,22,23,38]. However, some Amerindian tribes show genetic characters that do not accommodate with the suppositions of "homogeneity". Brown et al. [3] found a haplogroup X extensively distributed in America and present in Asia only in the Altaians of South-Central Siberia [10]. Even when there is not conclusive evidence that Amerindians have more than one ancestor – non-Asians – the Amerindian diversity does not seem to be completely derived from the Asiatic one.

By other hand, if the double-migratory event (Paleoamerican and Amerindian) for the main part of the Americas is accepted, the eventual genetic relationships between both waves must be discussed. Morphologic divergence between Paleoamericans and Amerindians would suggest that the former have not originated or at least did not genetically contributed to the later [19,25,26,36]. However, Powell and Neves [29] proposed that micro evolutionary processes could be responsible for that morphologic divergence. It is also probable that some South American groups are direct descendants of Paleoamericans as it was suggested for the Pericúes of Baja California in Mexico [13].

Options (c), (d) and (e) are proposed by the genetic neutral models. Options (c) and (d) do not seem probable: according with Rogers et al. [33], the hunter-gatherers increase very rarely their population size in a short period of time moreover during climatic instability. Steele et al. [37] developed a model for Paleoamerican dispersion in North America during the Pleistocene-Holocene transition and they deduced that it was not followed by an increase of the population size.

Option (e) is partially related with population size. The archaeological record shows that around 13000 BP South America was widely occupied. Due to the arid conditions after 13000 BP, populations would remain near waterways sites limiting their mobility [8]. Thus, the fragmentation of the geographic range would contribute to variation through genetic drift.

The option (f) was exceptionally mentioned [17,21] and it is discarded. The effect of environmental factors on morphologic traits is not denied but its contribution to inflate or reduce the distances among populations has not been proved. Moreover, it is difficult to understand why the environmental pressure would be greater in the Americas than in any other region.

5. Conclusions

These results show a high level of craniometric diversity among the southern Amerindians. This fact would result by different but not exclusive processes: (1) a low population size of first migrants followed by a great dispersion in different and unstable environments; (2) the genetic contribution of the ancient Paleoamericans to the most modern Amerindians; (3) many migratory waves coming from different geographic regions; and (4) an old settlement (older than 13 000 yr) of Americas. The high craniometrical variation found in this study is insufficient to solve the problem of their evolution but it constitutes an element that questions the established idea about Amerindians.

Acknowledgements

This work has been possible by Scholarships of the Universidad Nacional de La Plata (Argentina) and a Fondation Fyssen Grant held by MLS and by the French-Argentine cooperation CNRS–CONICET: *La place des Amérindiens face au contexte morphologique et géographique de l'Eurasie*.

References

[1] L.A. Borrero, C. Mc Ewan, The peopling of Patagonia. The first human occupation, in: C. Mc Ewan, L.A. Borrero, A. Prieto (Eds.), Patagonia. Natural History, Prehistory and Ethnography at the Uttermost End of the Earth, British Museum Press, London, 1997, pp. 32–45.

[2] C.L. Brace, A.R. Nelson, N. Seguchi, H. Oe, L. Sering, P. Qifeng, L. Yongyi, D. Tumen, Old World sources of the first New World human inhabitants: a comparative craniofacial view, Proc. Natl Acad. Sci. USA 98 (2001) 10017–10022.

[3] M.D. Brown, S.H. Hosseini, A. Torroni, H.J. Bandelt, J.C. Allen, T.G. Schurr, R. Scozzari, F. Cruciani, D.C. Wallace, mtDNA haplogroup X: an ancient link between Europe/Western Asia and North America? Am. J. Hum. Genet. 63 (1998) 1852–1861.

[4] R. Casamiquela, Los pueblos indígenas, Ciencia Hoy 2 (1990) 18–28.

[5] J.N. Darroch, J.E. Mossiman, Canonical and principle components of shape, Biometrika 72 (1985) 241–252.

[6] R. Deka, M.D. Shriver, L.M. Yu, R.E. Ferrell, R. Chakraborty, Intra- and inter-population diversity at short tandem repeat loci in diverse populations of the world, Electrophoresis 16 (1995) 1659–1664.

[7] E.J. Devor, Transmission of human craniofacial dimensions, J. Craniofacial Genet. Dev. Biol. 7 (1987) 95–106.

[8] T. Dillehay, The settlement of the Americas. A new prehistory, Basic Books, New York, 2000.

[9] R.D. Easton, D.A. Merriwether, D.E. Crews, R.E. Ferrell, mtDNA variation in the Yanomami: evidence for additional New World founding lineages, Am. J. Hum. Genet. 59 (1996) 213–225.

[10] J.A. Eshleman, R.S. Malhi, D.G. Smith, Mitochondrial DNA studies of native Americans: conceptions and misconceptions of the population prehistory of the Americas, Evol. Anthropol. 12 (2003) 7–18.

[11] P. Forster, R. Harding, A. Torroni, H.J. Bandelt, Origin and evolution of Native American mtDNA variation: a reappraisal, Am. J. Hum. Genet. 59 (1996) 935–945.

[12] J. Gómez Otero, J.L. Lanata, A. Prieto, Arqueología de la costa atlántica patagónica, Rev. Arqueol. Am 15 (1998) 107–185.

[13] R. González-José, A. González-Martín, M. Hernández, H.M. Pucciarelli, M. Sardi, A. Rosales, S. van der Molen, Craniometric evidence for Paleoamerican survival in Baja California, Nature 425 (2003) 62–65.

[14] J.M. Greenberg, C.G. Turner II, S.L. Zegura, The settlement of the Americas: comparison of the linguistic, dental and genetic evidence, Curr. Anthropol. 27 (1986) 477–497.

[15] R. Gruhn, The Pacific coast route of initial entry: an overview, in: R. Bonnichsen, D.G. Steele (Eds.), Method and Theory for Investigating the Peopling of the Americas, Center for the Study of the First Americans, Oregon, 1994, pp. 249–256.

[16] N. Guidon, G. Delibrias, Carbon-14 dates point to man in the Americas 32 000 years ago, Nature 321 (1986) 769–771.

[17] M. Hernández, C. Lalueza, C. García-Moro, Fueguian cranial morphology: the adaptation to a cold, harsh environment, Am. J. Phys. Anthropol. 103 (1997) 103–117.

[18] W.W. Howells, Cranial Variation in Man, Papers of the Peabody Museum of Archaeology and Ethnology, Harvard University Press, Cambridge, 1973.

[19] R.L. Jantz, D.W. Owsley, Variation among early North American crania, Am. J. Phys. Anthropol. 114 (2001) 146–155.

[20] A.G. Kozintsev, A.V. Gromov, V.G. Moiseyev, Collateral relatives of American indians among the Bronze Age populations of Siberia?, Am. J. Phys. Anthropol. 108 (1999) 193–204.

[21] M.M. Lahr, Patterns of modern human diversification: implications for Amerindian origins, Yearb. Phys. Anthropol. 38 (1995) 163–198.

[22] D.A. Merriwether, W.W. Hall, A. Vahlne, R.E. Ferrell, mtDNA variation indicates Mongolia may have been the source for the founding population for the New World, Am. J. Hum. Genet. 59 (1996) 204–212.

[23] J.V. Neel, R.J. Biggar, R.I. Sukernik, Virologic and genetic studies relate Amerind origins to the indigenous people of the Mongolia/Manchuria/southeastern Siberia region, Proc. Natl Acad. Sci. USA 91 (1994) 10737–10741.

[24] M. Nei, A.K. Roychoudhury, Evolutionary relationships of human populations on a global scale, Mol. Biol. Evol. 10 (1993) 927–943.

[25] W.A. Neves, H.M. Pucciarelli, Extra-continental biological relationships of early South-American human remains: a multivariate analysis, Ciência e Cultura 41 (1989) 566–575.

[26] W.A. Neves, H.M. Pucciarelli, Morphological affinities of the first Americans: An exploratory analysis based on early South American human remains, J. Hum. Evol. 21 (1991) 261–273.

[27] J. Nichols, Linguistic diversity and the first settlement of the New World, Language 66 (1990) 475–521.

[28] R.L. Parr, S.W. Carlyle, D.H. O'Rourke, Ancient DNA analysis of Fremont Amerindians of the Great Salt Lake Watland, Am. J. Phys. Anthropol. 99 (1996) 507–518.

[29] J.F. Powell, W.A. Neves, Craniofacial morphology of the first Americans: pattern and process in the peopling of the New World, Yearb. Phys. Anthropol. 42 (1999) 153–188.

[30] J.H. Relethford, Global Analysis of regional differences in craniometric diversity and population substructure, Hum. Biol. 73 (2001) 629–636.

[31] J.H. Relethford, J. Blangero, Detection of differential gene flow from patterns of quantitative variation, Hum. Biol. 62 (1990) 5–25.

[32] J.H. Relethford, H.C. Harpending, Craniometric variation, genetic theory and modern human origins, Am. J. Phys. Anthropol. 95 (1994) 249–270.

[33] R.A. Rogers, L.A. Rogers, L.D. Martin, How the door opened: the peopling of the New World, Hum. Biol. 64 (1992) 281–302.

[34] M.L. Sardi, Diferenciacion Craneofacial en Aborígenes de Patagonia y su Relación con Grupos Americanos y Extra-Americanos, Doctoral Tesis Dissertation, Universidad Nacional de La Plata, Argentina, 2002.

[35] T.G. Schurr, S.W. Ballinger, Y.Y. Gan, J.A. Hodge, D.A. Merriwether, D.N. Lawrence, W.C. Knowler, K.M. Weiss, D.C. Wallace, Amerindian mitochondrial DNAs have rare Asian mutations at high frequencies, suggesting they derived from four primary maternal lineages, Am. J. Hum. Genet. 46 (1990) 613–623.

[36] D.G. Steele, J.F. Powell, Paleobiological evidence of the peopling of the Americas: a morphometric view, in: R. Bonnichsen, D.G. Steele (Eds.), Method and Theory for Investigating the People of the Americas, Center for the Study of the First Americans, Oregon, 1994, pp. 141–163.

[37] J. Steele, J. Adams, T. Sluckin, Modelling paleoindian dispersals, World Archaeol. 30 (1998) 286–305.

[38] R.I. Sukernik, T.G. Shur, E.B. Starikovskaia, D.K. Uolles, Mitochondrial DNA variation in native inhabitants of Siberia with reconstructions of the evolutional history of the American Indians, Restriction polymorphism, Genetika 32 (1996) 432–439.

[39] L.M. Torres, Los Primitivos Habitantes del Delta del Paraná, Universidad Nacional de La Plata, Buenos Aires, 1911.