

## Mitochondrial DNA Polymorphism in Three Brazilian Indian Tribes

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**ABSTRACT** The first 360 base pairs of the mitochondrial DNA (mtDNA) major noncoding region from 82 individuals affiliated with the Brazilian Xavante, Zoró and Gavião tribes were sequenced. A total of 14 different lineages were observed, the largest number (8) being found among the Zoró. The latter share five lineages with the Gavião (who are their neighbors and are culturally similar to them), but only one with the Xavante. The lineages can be grouped into four clusters, previously identified by other authors. The 9 base pair deletion characteristic of Asian and Pacific populations occurs in 32% of the individuals, whose mtDNA was classified in five lineages, all grouped in one of the four clusters. Nucleotide diversity, as evaluated by three indices, are not much different from those observed in Indians from Central and North America, despite the fact that the Xavante consistently show lower numbers. These results do not confirm previous generalizations about the genetic diversity of Amerindians, and the need for additional studies in this system is stressed. © 1996 Wiley-Liss, Inc.

Studies at the protein level have disclosed different patterns of variation among American Indians. For instance, Bhathia et al. (1995), examining the distribution of Class I HLA antigens in South Amerindians, could not disclose clusters with internally consistent geographic or linguistic trends. But Rothhammer and Silva (1992), based on 13 marker systems and using principal components analysis coupled with computer-generated maps, detected clines that would validate models of population displacement based on archeological data. In the same direction, Callegari-Jacques et al. (1993), investigating the Gm haplotype distribution by correspondence factorial analysis and also using computer-generated maps, could detect clines both among North and South America.

The data available at the DNA level are much more restricted, although more is known about mitochondrial than nuclear DNA. In relation to the former (mtDNA),

questions have been centered on three issues: (a) the number of ancestral populations that colonized the New World; (b) the timing of their entry in the continent; and (c) the presence or absence of severe bottlenecks during the process of colonization. Using restriction fragment length polymorphisms (RFLPs) plus D-loop sequence analyses of part of the material, Wallace et al. (1985), Schurr et al. (1990), Torroni et al. (1992, 1993, 1994a), and Wallace and Torroni (1992) observed that all native American mtDNAs grouped into one of four distinct clusters, and postulated that a major genetic bottleneck occurred before the radiation of the ancestral Amerinds. The occurrence of such bottleneck, however, was questioned by

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Ward et al. (1991) and Horai et al. (1993), based on nucleotide sequence analysis of the mtDNA major noncoding region. Other RFLP, amplification and sequence studies of this region have recently been reported (Santos Pasamontes, 1992; Ginther et al., 1993; Shields et al., 1993; Santos and Barrantes, 1994; Santos et al., 1994; Monsalve et al., 1994; Merriwether et al., 1994; Lorenz and Smith, 1994; Kolman et al., 1995; Batista et al., 1995). Questions about the number of founding haplotypes and the epoch of the continent's colonization were addressed by Bailliet et al. (1994) and Torroni et al. (1994b), while Ward et al. (1993) considered the mtDNA and linguistic differentiation of three North American tribes. The significance of these findings has been evaluated by Szathmary (1993), Cann (1994, 1995), Torroni and Wallace (1995), Bianchi and Rothhammer (1995), and Rothhammer and Bianchi (1995).

The present report provides information about the variability of the mtDNA D-loop region in three Brazilian Indian tribes and considers in what way these new data contribute to the analysis of the questions indicated above.

#### MATERIALS AND METHODS

The populations sampled can be characterized as follows.

##### *Xavante*

They speak a Ge language, which can be assigned to the Macro-Ge subdivision of the Ge-Pano-Carib group (Rodrigues, 1986; Greenberg, 1987). Presently they live in six different areas delimited by the coordinates 51°10'W-54°5'W; 13°10'S-15°70'S. The village from which the material was collected is Rio das Mortes (51°40'W-13°20'S), situated near the western boundary of the Indian Reservation Pimentel Barbosa, State of Mato Grosso, Brazil. The Xavante have been in this general region since the nineteenth century. They arrived there from the east (area between the Araguaia and Tocantins rivers). Friendly contacts with non-Indians started in 1946 and were followed by colonization projects of the neo-Brazilian society that restricted their territory in marked degree. Starting in the 1970s, the Indians located in posts of the National Indian Foundation and in religious missions organized a reaction against this state of affairs that led to the successful recovery of most of these

lands, which were then demarcated as reservations for their use (Menezes, 1982). The Xavante experienced a marked population growth in the last decades. From an estimated number of 1,500-2,000 in the 1960s, they have grown to 6,233 individuals at present (Ricardo, 1991). Extensive genetic and biochemical studies have been performed among subjects of this tribe some years ago (Neel et al., 1964; Neel and Salzano, 1967; see the general review in Salzano and Callegari-Jacques, 1988). Afterwards, they were one of the four contrasting groups of Central Brazilian Indians chosen for the investigation of questions related to important human ecological problems (Werner et al., 1979; Gross et al., 1979; Flowers et al., 1982). The present study is a part of a wider project aimed at understanding the major biomedical changes that occurred in Pimentel Barbosa since the group was first visited in July 1962. Partial reports of these new investigations have been published (Alvarez et al., 1991; Friedman et al., 1992; Coimbra et al., 1992a, 1993; Flowers, 1994).

##### *Zoró*

Their language was classified in the Tupi stock, Mondé family (Rodrigues, 1986). They live in a single village, located 20 km from the Branco river (approximately 60°20'W; 10°20'S), Aripuanã Indian Park, State of Mato Grosso, Brazil. More extensive contacts with non-Indians only started in 1977 (Anonymous, 1978), and at that time it was estimated that they should number 350 persons. In July-August 1990, however, this number had been reduced to 215 (Santos, 1991). Several biomedical studies have been performed among them (Coimbra and Santos, 1989; Santos and Coimbra, 1991; Fleming-Moran et al., 1991; Coimbra et al., 1992b). An overall evaluation of these and other investigations can be found in Santos (1991).

##### *Gavião*

This Tupi-Mondé group should not be confounded with Ge-speaking groups with the same name living in southeast Pará (Gavião-Parkatejê) or Maranhão (Gavião-Pukobiê). The population studied actually lives somewhat further west than the Zoró, in the Indian Area Igarapé Lourdes, State of Rondônia, Brazil. They are distributed in two villages, but many of them have houses in both. Samples were obtained from people of

the two communities (geographical coordinates: 61°8'W; 10°10'S). In July–August 1990, the total population was estimated as 288 individuals (Santos, 1991). The Gavião were contacted by neo-Brazilians in the early 1940s and are much more acculturated than their neighbors, the Zoró; however, these two groups have several features in common, and have been investigated together (as well as with another Tupi-Mondé tribe, the Surui) as a model for the study of the effects of acculturation on health (Coimbra and Santos, 1989; Santos, 1991; Santos and Coimbra, 1991; Coimbra et al., 1992b, 1993).

Blood samples were refrigerated shortly after collection and sent by air to Porto Alegre, where DNA was extracted using the technique of Miller et al. (1988). Afterwards, aliquots of DNA were sent to Salt Lake City, where they were processed with methods already described (Ward et al., 1991). Nucleotide diversity ( $\pi$ ) values were calculated using the SEND program (Nei and Jin, 1989) and tree constructions were performed using the MEGA program (Kumar et al., 1993).

## RESULTS

Table 1 presents the nucleotide sequence differences observed in the first 360 base pairs of the control region in the mtDNA of the 82 individuals affiliated with the three tribes. A total of 14 different lineages were observed. The largest number was found among the Zoró (8); five of them occur also among the Gavião, who also present two lineages found only among them. The Zoró also share one lineage with the Xavante, and also show three unique sequences. Three of the lineages were previously observed in the Nuu-Chah-Nulth (Ward et al., 1991); the corresponding numbers are (the lineage number assigned in this study is given first; the second number is that given by the latter authors): 1 = 27; 4 = 11; 7 = 21. Lineage 1, therefore, occurs among the Xavante, Zoró and Nuu-Chah-Nulth. The nine base pairs deletion characteristic of some Asian and Pacific populations was observed in 26 (32%) of the 82 individuals, whose mtDNA was classified in lineages 1–3, 10 and 13. All nucleotide substitutions are transitions.

Additional information about the variability is provided in Table 2. Three diversity indices were calculated for these three newly studied groups, and for three others chosen for comparison (the Mapuche from Argen-

tina, within South America but outside Brazil; the Huetar from Costa Rica, thus living in Central America; and the Nuu-Chah-Nulth from Vancouver Island, Canada). The first index expresses gene diversity (an analog of heterozygosity), considering the sequences in the population. The second ( $\pi$ ) represents an average of the differences between sequences, while the third evaluates the number of polymorphic (segregating) sites per nucleotide site. This estimator is independent of type frequencies and measures a long-term average rather than a "current generation" value. The three indices vary in the same direction ( $r = 0.87–0.95$ ), with the Xavante showing the lowest numbers (0.68, 0.0084, 2.65), and the Mapuche and Nuu-Chah-Nulth the highest (0.91, 0.95; 0.0153, 0.0150; 4.97, 5.52).

Figure 1 presents a phylogenetic tree comparing the different lineages found in the three tribes. The tree was obtained using Jukes-Cantor distances, the neighbor-joining method and 2,000 bootstrap replications. The same results were found using UPGMA (unweighted pair-group method with arithmetic averaging) instead of the neighbor-joining method; or taking into consideration differing rates of changes per nucleotide (Jin and Nei, 1990). As observed repeatedly in previous investigations (Ward et al., 1991; Horai et al., 1993; Torroni et al., 1993), the lineages can be grouped into four clusters. Lineages 1, 2, 3, 10, and 13 (including, therefore, three of the four Xavante lineages) fall in Ward et al.'s (1991) cluster IV (I of Horai et al., 1993), which is the only one in which the nine pair deletion occurs. Lineages 6, 7, 9, and 12, shared by the Zoró and Gavião, can be included in Horai et al.'s (1993) cluster II (but in none of those identified by Ward et al., 1991). Lineages 4, 5 and 14, derived from the three tribes, are grouped in cluster II (Ward et al., 1991) or III (Horai et al., 1993), while lineages 8 and 11, present among the Zoró only, would be classified in clusters III (Ward et al., 1991) or IV (Horai et al., 1993). Therefore, the Xavante have lineages pertaining to only two of the four clusters, the Gavião to three and the Zoró to all four clusters.

A general genealogy comparing these lineages with those from the three other Amerindian populations listed in Table 2, as well as with others obtained in all continents (too extensive to be reproduced here), was also compiled using the method of Tamura and

TABLE 1. Nucleotide sequence differences in the major noncoding region of mtDNA from 82 individuals affiliated with three Brazilian Indian tribes

| Tribes and lineages | Nucleotide position in control region |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   | 9 | No. observed |   |   |    |   |    |
|---------------------|---------------------------------------|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|--------------|---|---|----|---|----|
|                     | 1                                     | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |   |              | 1 |   |    |   |    |
|                     | 6                                     | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 6 |   |              | 6 |   |    |   |    |
|                     | 0                                     | 0 | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 3 | 3 | 3 | 3 | 3            | 3 | d |    |   |    |
|                     | 9                                     | 9 | 1 | 6 | 7 | 8 | 1 | 2 | 4 | 5 | 6 | 6 | 7 | 8 | 9 | 9 | 9 | 0 | 1 | 1 | 2            | 2 | 6 | e  |   |    |
|                     | 2                                     | 3 | 1 | 8 | 5 | 9 | 7 | 3 | 1 | 6 | 1 | 6 | 8 | 4 | 0 | 1 | 8 | 4 | 6 | 9 | 5            | 7 | 2 | 1  |   |    |
| Reference sequence  | T                                     | T | C | C | A | T | T | C | A | C | C | C | C | A | C | C | T | T | A | G | T            | C | T | /  | / |    |
| Xavante             |                                       |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |              |   |   |    |   |    |
| 1                   | .                                     | . | . | . | . | C | C | . | . | . | . | . | . | . | . | . | . | . | . | . | .            | . | . | .  | f | 11 |
| 2                   | .                                     | . | . | T | . | C | C | . | . | . | . | . | . | . | . | . | . | . | . | . | .            | . | . | .  | + | 1  |
| 3                   | .                                     | C | . | . | . | C | C | . | G | . | . | . | . | . | . | . | . | . | . | . | .            | . | . | .  | + | 9  |
| 4                   | .                                     | . | T | . | . | . | . | T | . | . | . | . | . | . | T | . | . | . | A | . | .            | C | . | -  | 4 |    |
| Zoró <sup>1</sup>   |                                       |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |              |   |   |    |   |    |
| 5                   | .                                     | . | T | . | . | . | T | . | . | . | . | T | T | T | . | . | . | A | . | . | C            | . | - | 6  |   |    |
| 6                   | .                                     | . | . | . | . | C | T | . | . | . | . | . | . | . | . | C | . | . | C | . | C            | . | - | 2  |   |    |
| 7                   | .                                     | . | . | . | . | . | T | . | . | . | . | . | . | . | . | . | . | . | C | . | C            | . | - | 13 |   |    |
| 8                   | .                                     | C | . | . | . | . | T | . | . | . | . | . | . | . | . | C | . | . | . | C | T            | . | - | 3  |   |    |
| 9                   | .                                     | . | . | . | G | . | T | . | . | . | . | . | . | . | . | . | . | . | . | C | .            | C | - | 2  |   |    |
| 10                  | .                                     | . | . | . | . | C | . | . | . | . | . | . | . | . | . | . | G | . | . | . | .            | . | + | 1  |   |    |
| 11                  | .                                     | C | . | . | . | . | T | T | . | . | . | . | . | . | . | C | . | . | . | C | T            | . | - | 1  |   |    |
| 12                  | .                                     | . | . | . | . | C | T | . | . | . | . | . | . | . | . | . | . | . | . | C | .            | C | - | 1  |   |    |
| Gavião <sup>2</sup> |                                       |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |              |   |   |    |   |    |
| 13                  | .                                     | . | . | . | . | C | C | . | . | T | . | G | . | . | . | . | . | . | . | . | .            | . | . | +  | 4 |    |
| 14                  | C                                     | . | T | . | . | C | . | T | . | . | . | T | . | . | T | . | . | . | A | . | .            | C | . | 1  |   |    |

<sup>1</sup>One individual from the Zoró presents lineage 1 observed among 11 Xavante.  
<sup>2</sup>There is extensive lineage sharing between the Zoró and Gavião. Besides the two specific lineages the Gavião also present the following, found among the Zoró (number of individuals in parentheses): 5(3); 6(5); 7(5); 9(6); 12(3).

TABLE 2. mtDNA sequence diversity in three Brazilian Indian tribes, compared with data from other Amerindians, using the first 360 nucleotides of the control region

| Tribes                      | No. of individuals | No. of different lineages | Gene diversity ± S.E. <sup>1</sup> | Nucleotide diversity ± S.E. |                   |
|-----------------------------|--------------------|---------------------------|------------------------------------|-----------------------------|-------------------|
|                             |                    |                           |                                    | $\pi^2$                     | F(s) <sup>3</sup> |
| Xavante                     | 25                 | 4                         | 0.68 ± 0.03                        | 0.0084 ± 0.0028             | 2.65 ± 0.84       |
| Zoró                        | 30                 | 9                         | 0.78 ± 0.14                        | 0.0112 ± 0.0029             | 4.30 ± 1.04       |
| Gavião                      | 27                 | 7                         | 0.87 ± 0.00                        | 0.0112 ± 0.0032             | 4.15 ± 1.04       |
| All three                   | 82                 | 14                        | 0.89 ± 0.00                        | 0.0139 ± 0.0035             | 4.62 ± 0.96       |
| Mapuche <sup>4</sup>        | 39                 | 13                        | 0.91 ± 0.00                        | 0.0153 ± 0.0037             | 4.97 ± 1.08       |
| Huetar <sup>5</sup>         | 27                 | 7                         | 0.71 ± 0.04                        | 0.0098 ± 0.0033             | 3.11 ± 0.90       |
| Nuu-Chah-Nulth <sup>6</sup> | 63                 | 28                        | 0.95 ± 0.00                        | 0.0150 ± 0.0035             | 5.52 ± 1.08       |
| General total               | 211                | 56                        | 0.97 ± 0.00                        | 0.0155 ± 0.0014             | 7.59 ± 1.13       |

<sup>1</sup>Using formula 8.5 and 8.13 given in Nei (1987, pp. 179–180). Further information in the text.  
<sup>2</sup>Using formulas 2 and 3 given in Nei and Jin (1989). Further information in the text.  
<sup>3</sup>Using formulas 5–8 given in Tajima (1993, p. 572). Further information in the text.  
<sup>4</sup>Data from Ginther et al. (1993).  
<sup>5</sup>Data from Santos Pasamontes (1992).  
<sup>6</sup>Data from Ward et al. (1991).

Nei (1993), considering both the UPGMA and neighbor-joining procedures. The four clusters previously observed by all previous investigators were again found to be present, but outliers also occurred.

DISCUSSION

In a general way, the results obtained in the three Brazilian tribes are in accordance with those expected considering historical

and biodemographical data. The Xavante village that was studied has a past of a high degree of inbreeding and isolation due to the strong influence of a famous leader, Apewe, who kept its members under rigid control for decades (Neel et al., 1964). It has not been possible in the 1960s and in the recent field work to identify cases of introduction of women from other tribes into this community. The Zoró and Gavião show more

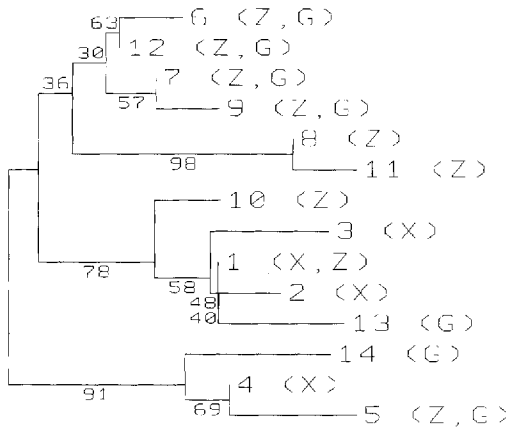


Fig. 1. Phylogenetic tree comparing the 14 lineages observed among the Xavante (X), Zoró (Z), and Gavião (G). Similar relationships were obtained with other methods, like maximum-parsimony and maximum likelihood. The numbers at the nodes represent bootstrap values.

mtDNA diversity and share a large number of lineages. Since they speak similar languages, have many cultural traits in common, and live in relatively close geographical proximity, their mtDNA similarity is not unexpected. As for the estimates of nucleotide diversity, the main impression obtained is that the three tribes are not very different from North, Central or South American Indians. The three indices follow similar trends, which are, however, independent of geographical location. It is difficult to compare the present figures with those of other authors, since the latter do not indicate the formulae used. Nevertheless, the three tribes described do not seem to be unusual in this regard.

Much more data than those presently available are necessary to establish more firm conclusions about the three questions mentioned in the introduction, i.e., the number of ancestral populations that colonized the New World, the timing of their entry in the continent, and the presence or absence of severe bottlenecks during the colonization process. For instance, the absence of the so-called Asian-specific nine base pair deletion (which occurs in high frequencies in Pacific populations as well) among the Ticuna was invoked by Schurr et al. (1990) as evidence in favor of their hypothesis that severe genetic restriction occurred during the process of col-

onization from North to South America. Horai et al. (1993), however, have observed that the deletion occurs in native populations from Colombia, Brazil and Chile; Ginther et al. (1993) found it among the Mapuche of Argentina, Torroni et al. (1993) among the Kraho and Mataco of Brazil and Argentina, respectively, and Merriwether et al. (1994) among the Aymara, Pehuenche, Huilliche and Atacameno of Chile, and the Quechua of Peru. It was also observed in the three tribes presently described. Horai et al. (1993), on the basis of the bimodal distribution of pairwise sequence differences observed among native Americans, also concluded that severe bottlenecks could not have occurred during the peopling of the New World. Similar analyses were made by Kolman et al. (1995) and Batista et al. (1995). Bimodal distributions were also obtained in the Xavante, Zoró and Gavião (data not shown), but a more thorough analysis of this problem is necessary. This analysis should take into consideration within and between clusters comparisons before a definitive interpretation can be reached.

The question of the number of New World founding populations merits consideration. Turner (1983, 1985), on the basis of dental evidence, and Greenberg et al. (1986), after consideration of linguistic, dental and monogenic blood systems, arrived at what has been called the "three-waves of migration" theory of colonization of the New World. The three founding groups would be the Paleo-Indians, the Na-Dene and the Eskimo-Aleuts, and they would have entered the continent in this order, starting 40,000-16,000 years ago. Torroni et al. (1992) found that the Amerinds (descendants of the postulated Paleo-Indians) and Na-Dene showed pronounced mtDNA differences which favors the hypothesis. However, Shields et al. (1993), also using mtDNA results, could not separate Na-Dene speaking groups from Eskimos. In addition, several lines of evidence (see Callegari-Jacques et al., 1993) indicate that to consider all Amerindians, with the exception of the Na-Dene, as a single biological entity, appears to be an oversimplification. The four mtDNA clusters monotonously observed by all researchers in these populations, and confirmed in the present study, are clearly against this view. Moreover, Baillet et al. (1994) convincingly suggested the existence of other founder lineages in addition to these four, and some of the outliers

observed in the present study (the general genealogy mentioned at the end of the results section) can be traced directly to Asia. On the other hand, tribal population structure is of such a nature (based on fissions and fusions, see Neel and Salzano, 1967) that the idea of large scale migrations of totally independent groups appears unwarranted.

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#### LITERATURE CITED

- Alvarez RR, Campbell J, Friedman H, Bertoli ML, Gama GBMN, Diaz LA (1991) Dermatose entre os Xavante da Área Indígena Pimentel Barbosa, Mato Grosso (Brasil). *Cad. Saúde Públ.* 7:581-584.
- Anonymous (1978) Apena conta atração dos Zoró. *Rev. Atual. Indig.* 2:2-8.
- Bailliet G, Rothhammer F, Carnesc FR, Bravi CM, Bianchi NO (1994) Founder mitochondrial haplotypes in Amerindian populations. *Am. J. Hum. Genet.* 55:27-33.
- Batista O, Kolman CJ, Bermingham E (1995) Mitochondrial DNA diversity in the Kuna Amerinds of Panamá. *Hum. Molec. Genet.* 4:921-929.
- Bhatia KK, Black FL, Smith TA, Prasad ML, Koki GN (1995) Class I HLA antigens in two long-separated populations: Melanesians and South Amerinds. *Am. J. Phys. Anthropol.* 97:291-305.
- Bianchi NO, Rothhammer F (1995) Reply to Torroni and Wallace. *Am. J. Hum. Genet.* 56:1236-1238.
- Callegari-Jacques SM, Salzano FM, Constans J, Maurières P (1993) Gm haplotype distribution in Amerindians: Relationship with geography and language. *Am. J. Phys. Anthropol.* 90:427-444.
- Cann RL (1994) mtDNA and native Americans: A southern perspective. *Am. J. Hum. Genet.* 55:7-11.
- Cann RL (1995) Reply to Rothhammer and Bianchi. *Am. J. Hum. Genet.* 56:1248.
- Coimbra CEA, Jr., Santos RV (1989) Black Piedra among the Zoró Indians from Amazônia (Brazil). *Mycopathologia* 107:57-60.
- Coimbra CEA, Jr., Borges MM, Flowers NM, Santos RV, Piazza RF (1992a) Sero-epidemiological survey for Chagas' disease among the Xavante Indians of Central Brazil. *Ann. Trop. Med. Parasitol.* 86:567-568.
- Coimbra CEA, Jr., Santos RV, Wanke B, Valle ACF, Costa RLB (1992b) Environmental changes and disease: The case of paracoccidioidomycosis among the Tupi Mondé Indians from the Brazilian Amazonia. *Am. J. Phys. Anthropol. Suppl.* 14:61 (abstract).
- Coimbra CEA, Jr., Santos RV, Yoshida CFY, Baptista ML, Flowers NM, Valle ACF, Mercadante LAC (1993) Hepatitis B epidemiology in four native populations from the Brazilian Amazon. *Am. J. Phys. Anthropol., Suppl.* 16:71-72 (abstract).
- Fleming-Moran M, Santos RV, Coimbra CEA, Jr. (1991) Blood pressure levels of the Surui and Zoró Indians of the Brazilian Amazon: Group- and sex-specific effects resulting from body composition, health status, and age. *Hum. Biol.* 63:835-861.
- Flowers NM (1994) Demographic crisis and recovery: A case study of the Xavante of Pimentel Barbosa. *South Am. Indian St.* 4:18-36.
- Flowers NM, Gross DR, Ritter ML, Werner DW (1982) Variation in swidden practices in four Central Brazilian Indian societies. *Hum. Ecol.* 10:203-217.
- Friedman H, Coimbra CEA, Jr., Alvarez RR, Campbell I, Diaz LA, Flowers NM, Santos RV, Bertoli ML, Gama GBMN, Alcalá MCO (1992) Pênfigo foliáceo endêmico (fogo-selvagem) no grupo indígena Xavante, Mato Grosso, Brasil. *Cad. Saúde Públ.* 8:331-334.
- Ginther C, Corach D, Penacino GA, Rey JA, Carnesc FR, Hutz MH, Anderson LE, Just J, Salzano FM, King MC (1993) Genetic variation among the Mapuche Indians from the Patagonian region of Argentina: Mitochondrial DNA sequence variation and allele frequencies of several nuclear genes. In SDJ Pena, R Chakraborty, JT Epplen, AJ Jeffreys (eds.): *DNA Fingerprints: State of the Art.* Basel: Birkhauser Verlag, pp. 211-219.
- Greenberg JH (1987) *Language in the Americas.* Stanford: Stanford University Press.
- Greenberg JH, Turner CG II, Zegura SL (1986) The settlement of Americas: A comparison of the linguistic, dental, and genetic evidence. *Curr. Anthropol.* 27:477-497.
- Gross DR, Eiten G, Flowers NM, Leoi FM, Ritter ML, Werner DW (1979) Ecology and acculturation among native peoples of Central Brazil. *Science* 206:1043-1050.
- Horai S, Kondo R, Nakagawa-Hattori Y, Hayashi S, Sonoda S, Takima K (1993) Peopling of the Americas, founded by four major lineages of mitochondrial DNA. *Mol. Biol. Evol.* 10:23-47.
- Jin L, Nei M (1990) Limitations of the evolutionary parsimony method of phylogenetic analysis. *Mol. Biol. Evol.* 7:82-102.
- Kolman CJ, Bermingham E, Cooke R, Ward RL, Arias TD, Guionneau-Sinclair F (1995) Reduced mtDNA diversity in the Ngöbé Amerinds of Panamá. *Genetics* 140:275-283.
- Kumar S, Tamura K, Nei M (1993) MEGA: Molecular Evolutionary Analysis Program, Version 1.01. University Park: The Pennsylvania State University.
- Lorenz JG, Smith DG (1994) Distribution of the 9-bp mitochondrial DNA region V deletion among North American Indians. *Hum. Biol.* 66:777-788.

- Menezes C (1982) Os Xavante e o movimento de fronteira no leste matogrossense. *Rev. Antropol.* 25:63–87.
- Merriwether DA, Rothhammer F, Ferrell RE (1994) Genetic variation in the New World: Ancient teeth, bone, and tissue as sources of DNA. *Experientia* 50:592–601.
- Miller SA, Dykes DD, Polesky HF (1988) A simple salting out procedure for extracting DNA from human nucleated cells. *Nucl. Acids Res.* 16:1215.
- Monsalve MV, Groot de Restrepo H, Espinel A, Correal G, Devine DV (1994) Evidence of mitochondrial DNA diversity in South American aboriginals. *Ann. Hum. Genet.* 58:265–273.
- Neel JV, Salzano FM (1967) Further studies on the Xavante Indians. X. Some hypotheses-generalizations resulting from these studies. *Am. J. Hum. Genet.* 19:554–574.
- Neel JV, Salzano FM, Junqueira PC, Keiter F, Maybury-Lewis D (1964) Studies on the Xavante Indians of the Brazilian Mato Grosso. *Am. J. Hum. Genet.* 16:52–140.
- Nei M (1987) *Molecular Evolutionary Genetics*. New York: Columbia University Press.
- Nei M, Jin L (1989) Variances of the average numbers of nucleotide substitutions within and between populations. *Mol. Biol. Evol.* 6:290–300.
- Ricardo CA (1991) *Povo Indígenas no Brasil (1987/88/89/90)*. São Paulo: Centro Ecumênico de Documentação e Informação.
- Rodrigues AD (1986) *Línguas Brasileiras. Para o Conhecimento das Línguas Indígenas*. São Paulo: Edições Loyola.
- Rothhammer F, Bianchi NO (1995) Origin and distribution of B mtDNA lineage in South America. *Am. J. Hum. Genet.* 56:1247–1248.
- Rothhammer F, Silva C (1992) Gene geography of South America: Testing models of population displacement based on archeological evidence. *Am. J. Phys. Anthropol.* 89:441–446.
- Salzano FM, Callegari-Jacques SM (1988) *South American Indians. A Case Study in Evolution*. Oxford: Clarendon Press.
- Santos M, Barrantes R (1994) D-loop mtDNA deletion as a unique marker of Chibchan Amerindians. *Am. J. Hum. Genet.* 55:413–414.
- Santos M, Ward RH, Barrantes R (1994) mtDNA variation in the Chibcha Amerindian Huetar from Costa Rica. *Hum. Biol.* 66:963–977.
- Santos RV (1991) *Coping with change in native Amazonia: A bioanthropological study of Gavião, Surui, and Zoró, Tupi-Mondé speaking societies from Brazil*. Doctoral dissertation, Department of Anthropology, Indiana University, Bloomington.
- Santos RV, Coimbra CEA Jr. (1991) Socioeconomic transition and physical growth of Tupi-Mondé Amerindian children of the Aripuanã Park, Brazilian Amazon. *Hum. Biol.* 63:795–819.
- Santos Pasamontes M (1992) *Análisis de variación genética del ADNmt y nuclear de una población amerindia, Huetar, Costa Rica*. MSc dissertation, Escuela de Biología, Universidad de Costa Rica, San José.
- Schurr TG, Ballinger SW, Gan YY, Hodge JA, Merriwether DA, Lawrence DN, Knowler WC, Weiss KM, Wallace DC (1990) Amerindian mitochondrial DNAs have rare Asian mutations at high frequencies, suggesting they derived from four primary maternal lineages. *Am. J. Hum. Genet.* 46:613–623.
- Shields GF, Schmiechen AM, Frazier BL, Redd A, Voevoda MI, Reed JK, Ward RH (1993) mtDNA sequences suggest a recent evolutionary divergence for Beringian and northern North American populations. *Am. J. Hum. Genet.* 53:549–562.
- Szathmary EJE (1993) mtDNA and the peopling of the Americas. *Am. J. Hum. Genet.* 53:793–799.
- Tajima F (1993) Statistical analysis of DNA polymorphism. *Japan. J. Genet.* 68:567–595.
- Tamura K, Nei M (1993) Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. *Mol. Biol. Evol.* 10:512–526.
- Torrioni A, Wallace DC (1995) mtDNA haplogroups in native Americans. *Am. J. Hum. Genet.* 56:1234–1236.
- Torrioni A, Schurr TG, Yang CC, Szathmary EJE, Williams RC, Schanfield MS, Troup GA, Knowler WC, Lawrence DN, Weiss KM, Wallace DC (1992) Native American mitochondrial DNA analysis indicates that the Amerind and Nadene populations were founded by two independent migrations. *Genetics* 130:153–162.
- Torrioni A, Schurr TG, Cabell MF, Brown MD, Neel JV, Larsen M, Smith DG, Vullo CM, Wallace DC (1993) Asian affinities and continental radiation of the four founding native American mtDNAs. *Am. J. Hum. Genet.* 53:563–590.
- Torrioni A, Neel JV, Barrantes R, Schurr TG, Wallace DC (1994a) Mitochondrial DNA “clock” for the Amerinds and its implications for timing their entry into North America. *Proc. Natl. Acad. Sci. USA* 91:1158–1162.
- Torrioni A, Chen Y-S, Somino O, Santachiara-Beneceretti AS, Scott CR, Lott MT, Winter M, Wallace DC (1994b) mtDNA and Y-chromosome polymorphisms in four native American populations from southern Mexico. *Am. J. Hum. Genet.* 54:303–318.
- Turner CG II (1983) Dental evidence for the peopling of the Americas. In R Shuttler Jr. (ed): *Early Man in the New World*. Beverly Hills, CA: Sage Publications, pp. 147–157.
- Turner CG II (1985) The dental search for Native American origins. In R Kirk, E Szathmary (eds): *Out of Asia*. Canberra: Journal of Pacific History, pp. 31–78.
- Wallace DC, Garrison K, Knowler WC (1985) Dramatic founder effects in Amerindian mitochondrial DNAs. *Am. J. Phys. Anthropol.* 68:149–155.
- Wallace DC, Torrioni A (1992) American Indian prehistory as written in the mitochondrial DNA: A review. *Hum. Biol.* 64:403–416.
- Ward RH, Frazier BL, Dew-Jager K, Pääbo S (1991) Extensive mitochondrial diversity within a single Amerindian tribe. *Proc. Natl. Acad. Sci. USA* 88:8720–8724.
- Ward RH, Redd A, Valencia D, Frazier B, Pääbo S (1993) Genetic and linguistic differentiation in the Americas. *Proc. Natl. Acad. Sci. USA* 90:10663–10667.
- Werner D, Flowers NM, Ritter ML, Gross DR (1979) Subsistence productivity and hunting effort in native South America. *Hum. Ecol.* 7:303–315.