Color and genomic ancestry in Brazilians

Flavia C. Parra*, Roberto C. Amado†, José R. Lambertucci‡, Jorge Rocha§, Carlos M. Antunes†, and Sérgio D. J. Pena*¶

Departamentos de *Bioquímica e Imunologia and †Parasitologia, and ‡Faculdade de Medicina, Universidade Federal de Minas Gerais, 31270-901 Belo Horizonte, Brazil; and §Instituto de Patologia e Imunologia Molecular da Universidade do Porto, 4200 Porto, Portugal

This work was undertaken to ascertain to what degree the physical appearance of a Brazilian individual was predictive of genomic African ancestry. Using a panel of 10 population-specific alleles, we assigned to each person an African ancestry index (AAI). The procedure was able to tell apart, with no overlaps, 20 males from northern Portugal from 20 males from São Tomé Island on the west coast of Africa. We also tested 10 Brazilian Amerindians and observed that their AAI values fell in the same range as the Europeans. Finally, we studied two different Brazilian population samples. The first consisted of 173 individuals from a rural South-eastern community, clinically classified according to their Color (white, black, or intermediate) with a multivariate evaluation based on skin pigmentation in the medial part of the arm, hair color and texture, and the shape of the nose and lips. In contrast to the clear-cut results with the African and European samples, our results showed large variances and extensive overlaps among the three Color categories. We next embarked on a study of 200 unrelated Brazilian white males who originated from cosmopolitan centers of the four major geographic regions of the country. The results showed AAI values intermediate between Europeans and Africans, even in southern Brazil, a region predominantly peopled by European immigrants. Our data suggest that in Brazil, at an individual level, color, as determined by physical evaluation, is a poor predictor of genomic African ancestry, estimated by molecular markers.

> You see leaders today, all over the world, doing it again!
> Black, white, yellow, brown, people of every color
> slaughtering people of every color! Because Satan is
> always the same.
>
> S. L. Carter (1)

There is wide agreement among anthropologists and human geneticists that, from a biological standpoint, human races do not exist (2, 3). Yet, races do exist as social constructs that are mutable over time and across social contexts and are sustained by a racial ideology (4). The physical traits of an individual, especially skin pigmentation, hair color, hair texture, and the shape of the lips and nose, are constantly used for racial categorization and thus play an extremely influential role in human social relationships. However, these oligogenic traits are believed to have emerged as adaptations to geographical selective factors such as solar radiation and heat (5, 6) and their utilization as markers of "race" is erroneous. Still, regardless of its biological meaning, skin color matters a great deal. In a 2001 essay, then President William J. Clinton initially agreed with W. E. B. Dubois in that "the problem of the 20th century is the problem of the color line" (7). He then went on to condemn racial profiling and to hope that in the 21st century color differences could be transformed from a problem into a promise for America (7). Of course, the social importance of skin color is not by any means an exclusively American phenomenon; racial discrimination and conflict occur worldwide.

In Brazil, not withstanding relatively large levels of genetic admixture and a myth of "racial democracy," there exists a widespread social prejudice that seems to be particularly connected to the physical appearance of the individual (8). Color (in Portuguese, cor) denotes the Brazilian equivalent of the English term race (raça) and is based on a complex phenotypic evalu-ation that takes into account, besides skin pigmentation, hair type, nose shape, and lip shape (4, 9). The reason the word Color (capitalized to call attention to this particular meaning) is preferred to race in Brazil is probably because it captures the continuous aspects of phenotypes (4). In contrast with the situation in the United States, there appears to be no racial descent rule operational in Brazil and it is possible for two siblings differing in Color to belong to completely diverse racial categories (8). The Brazilian emphasis on physical appearance rather than ancestry is demonstrated by the fact that in a large survey when asked about their origins (the question admitted multiple responses) <10% of Brazilian black individuals gave Africa as one of their answers (10).

We wanted to ascertain to what degree the Color of a Brazilian individual was predictive of the degree of genomic African ancestry. To evaluate the latter we typed each person with a panel of 10 population-specific alleles (PSAs), i.e., alleles with wide frequency differentials (>48%) between Africa and Europe, developed by Parra et al. (11). With these data we could calculate a personal likelihood-ratio estimator of African ancestry (12) for individuals belonging to different Brazilian Color categories. The results demonstrated that at the individual level there was significant dissociation of Color, determined by physical evaluation, and African ancestry, estimated by molecular markers.

Materials and Methods

Populations Studied. We estimated the extent of African ancestry in two Brazilian population samples. The first was collected as part of an epidemiological study of schistosomiasis and included 173 individuals from the rural community of Queixadinha (17.12 south; 41.42 west) in the Vale do Jequitinhonha region of the state of Minas Gerais in Brazil (Fig. 1). They were all inhabitants of the same small village, which consisted of virtually a one-class community. Each individual was examined clinically and Color was established by using a multivariate evaluation based on skin color in the medial part of the arm, hair color and texture, and the shape of the nose and lips (Table 1). The format of the nose and lips were determined by direct comparison with depicted models from a human morphologic atlas (13). Two health workers evaluated each individual: those with white skin, straight or wavy hair, prominent or upturned nose tip, thin or median lips, independently of hair or eye pigmentation, were called white, whereas those with black skin, black curly hair, black eyes, and thick lips were classified as black. All other patients, including those for whom there was any doubt or disagreement between the two examiners, were classed as intermediate. Twenty-nine individuals were classified as white, 30 as black, and 114 as intermediate. Informed consent was obtained from all individuals studied.

We also studied 200 unrelated Brazilian males self-defined as whites, randomly drawn from paternity casework. This is the same sample described in our previous article (14). The individuals were from the following Brazilian regions (Fig. 1): 49

GENETICS

Fig. 1. Geographic localization of Brazilian localities selected for study: north region (states of Amazonas, Acre, Rondônia, and Pará), northeast region (Pernambuco), southeast region (Minas Gerais), and south region (Paraná, Santa Catarina, and Rio Grande do Sul). In the state of Minas Gerais (southeast) the approximate location of Queixadinha is indicated (⊗).

from the north (states of Amazonas, Acre, Rondônia, and Pará), 49 from the northeast (state of Pernambuco), 50 from the southeast (state of Minas Gerais), and 52 from the south (states of Rio Grande do Sul, Santa Catarina, and Paraná). Discrepancies in numbers were caused by geographical reclassification of two samples.

Additionally, we typed three samples of populations considered representative of the major founding groups of Brazil. The first, representing Europe, encompassed 20 individuals randomly drawn from the previously described (14) sample of 93 unrelated Portuguese men from the Porto District in northern Portugal (41.11 north; 8.36 west). The second, representing Africa, comprised 20 individuals from the town of Santana in São Tomé Island on the west coast of Africa (1.00 north; 7.00 east). Because this island was a Portuguese entrepôt for assembly of slaves before shipment to Brazil, its population had geographical origin in several regions of Africa (15). The population-based estimate of European genetic contribution to the Santana population was only 0.074 ± 0.015 (15). Finally, we studied a small Amerindian sample consisting of 10 individuals from three Amazonian tribes (Karitiana, Suruí, and Ticuna), all kindly provided by Judith Kidd (Yale University, New Haven, CT).

Table 1. Morphological trait evaluation for establishment of color

Skin pigmentation in the interior part of the forearm			
White	Brown	Black	
Hair type			
Straight	Wavy	Curly	
Hair color			
Blond	Brown	Black	Red
Eye pigmentation			
Blue	Green	Brown	Black
Nose conformation			
Prominent or upturned tip		Depressed tip	Flat
Lip conformation			
Thin	Median	Thick	

DNA Analysis. Blood was drawn, DNA was extracted, and each patient was then independently typed with the 10 PSAs defined by Parra *et al.* (11) as follows: *APO*, *AT3–I/D*, *GC*1S*, *GC*1F*, *FY–null*, *LPL*, *OCA 2*, *RB 2300*, *Sb19.3*, and *ICAM1*. With the exception of two Alu insertions polymorphism (*APO* and *Sb19.3*) and a polymorphic insertion of a 68-bp fragment at locus *AT3-I/D*, all other markers are single nucleotide polymorphisms and (except for *ICAM1*) were studied by digestion with the appropriate restriction enzyme after PCR, as described by Parra *et al.* (11). Typing at the *ICAM1* polymorphism was achieved by single-strand conformational polymorphism (16). After addition of 2.0 vol of a denaturing solution (100% formamide with 5 mg/ml dextran blue 2000), PCR products were denatured at 95°C for 5 min, and the mixture was applied in a native 10% polyacrylamide gel (18 × 17 × 0.1 cm), 0.5× Tris-borate·EDTA buffer (TBE) with 10% glycerol, subjected to electrophoresis in 1.0× TBE at 15 W for 5 h at room temperature, and then silver-stained according to Santos *et al.* (17). As standard, we used an African DNA sample homozygous for the rare allele.

Based on these results we assigned to each subject an individual African ancestry index (AAI) that was calculated as the logarithm of the ratio of the likelihood of a given multilocus genotype occurring in the African population to the likelihood of it occurring in the European population. Thus, the AAI represents a personal geographical ancestry estimate (12). For the likelihood ratio calculations we used the African and European allele frequencies given by Parra *et al.* (11).

Data Analysis. Allele frequencies were estimated by the gene counting method. Admixture proportions of each population sample were estimated with two methods. The first used the program ADMIX, which is based on a weighted least-square method (18) and was kindly made available by Jeffrey C. Long, University of Michigan, Ann Arbor. We also obtained point estimates of admixtures by using the graphical method (also based on difference minimization) described by Collins-Schramm *et al.* (19).

For comparison of two samples we used the Mann–Whitney *U* test and applied Bonferroni's correction for multiple comparisons (20). For correlations we used Spearman's rank correlation test (20).

Results

Europeans, Africans, and Amerindians. We examined the discrimination power of the 10-allele PSA set by initially studying a sample of 20 males from northern Portugal and 20 males from São Tomé Island in the Gulf of Guinea, on the west coast of Africa. These population sources were chosen because they are geographically related to the European and African population groups that participated in the peopling of Brazil. The box plot obtained from these data is shown in Fig. 2. There is no overlap between the two groups and >21 logs separating the two medians (9.71 and −11.73, respectively). As expected, the Mann–Whitney test was highly significant ($z = -5.4$, $P < 0.0001$). A complete individual discrimination between the European and African genomes was obtained with an existence of 7.6 logs between the lower African value (AAI = 2.86) and the highest European score (AAI = −4.86). It was thus clear that the 10-allele set of Parra *et al.* (11) was highly efficient and provided reliable individual discrimination between European and African genomes.

Brazilians constitute a trihybrid population with European, African, and Amerindian roots. Thus, we had to ascertain where the Amerindians would be positioned in reference to the AAI scale. For that, we tested DNA samples from 10 individuals from three Amazonian tribes (Karitiana, Suruí, and Ticuna) and observed that they fell in the same range as the Europeans, with AAIs varying from −2.77 to −12.57 and with a median of
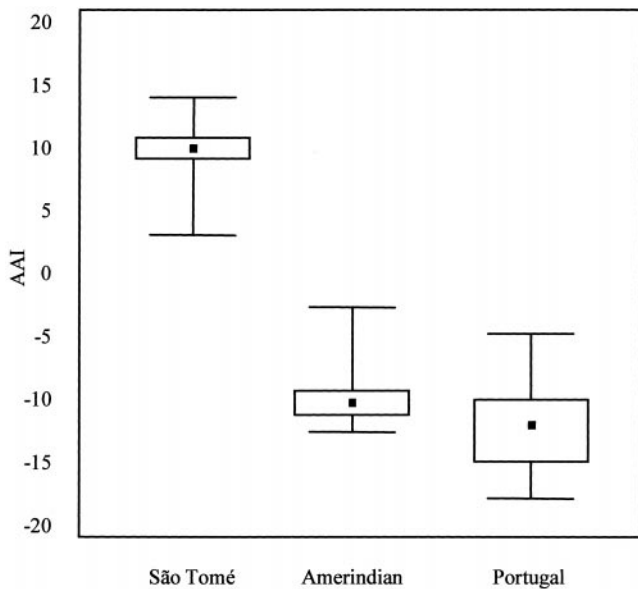
Fig. 2. Box plot graph showing the distribution of values of AAI in samples of the northern Portuguese population (*n* = 20), Africans from São Tomé Island (*n* = 20), and Amerindians (*n* = 10). Each group is represented as a box whose top and bottom are drawn at the lower and upper quartiles, with a small square at the median. Thus, the box contains the middle half of the scores in the distribution. Vertical lines outside the box extend to the largest and the smallest observations within 1.5 interquartile ranges from the box (20).

Fig. 3. Slot plot graphic [GraphPad (San Diego) PRISM software, version 2.01] of the AAIs from the three rural samples grouped according to their phenotype (30 black, 114 intermediate, and 29 white individuals) as well as from two of the Brazilian parental populations (20 Africans from São Tomé and 20 Europeans from Northern Portugal). Each symbol indicates the AAI value from one individual.

−10.18 (see Fig. 2). This finding is not unexpected, because several of the population-specific alleles in Parra's set had diverging frequencies in Europe and Africa because of specific selective factors operating in the African environment (11). Amerindians, who are well known to have a distant Asian ancestry, did not share such environments and would thus be expected to have frequencies similar to Europeans.

Brazilians. Our first Brazilian sample was composed of 173 individuals from a Southeastern rural community, clinically classified according to their Color (white, black, or intermediate) with a multivariate evaluation based on skin pigmentation in the medial part of the arm, hair color and texture, and the shape of the nose and lips. When we compared the AAI values for these individuals, we observed that the groups had much wider ranges than those of Europeans and Africans (Fig. 3) and that there was very significant overlap between them. For instance, one black individual had the fourth lowest (least African) AAI score (−10.48) whereas another individual, classified as intermediate, had the highest (most African) observed AAI (11.31). However, the comparison of whites versus blacks with the Mann–Whitney *U* test still showed a modest significant value ($z = 2.62; P < 0.01$). On the other hand, comparisons of whites versus the Portuguese and blacks versus São Tomé islanders yielded extremely high significance (respectively, $z = 5.08, P < 0.0001$ and $z = −5.24, P < 0.0001$), even after applying the Bonferroni correction for multiple comparisons (20). Thus, the differences in AAI values of the group of Brazilian blacks compared with Brazilian whites are very discrete and several orders of magnitude smaller than the differences observed between Africans and Europeans. We used the software STRUCTURE (21) to calculate the inferred proportion of African ancestry of each individual in our sample. There was a highly significant correlation between the two admixture estimates, thus further validating our AAI.

Of course, these results could not be naively extrapolated to all of Brazil. First, we had examined only a population of the
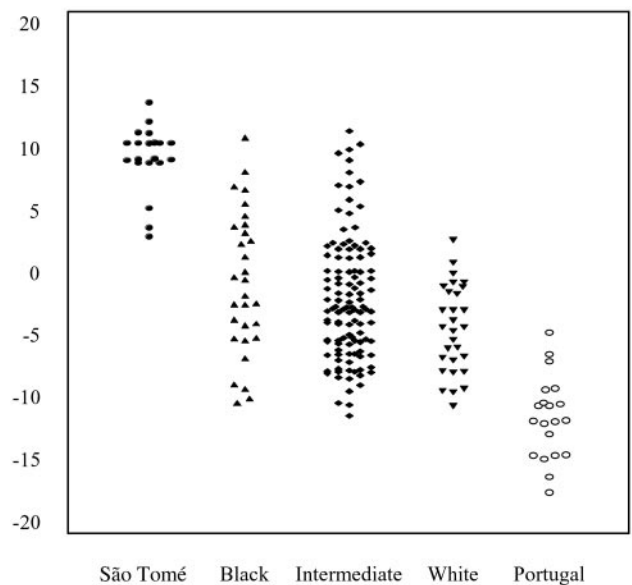
state of Minas Gerais, where European-African interbreeding occurred very intensely (22). Moreover, our samples were from a poor rural zone of the state, with negligible social stratification. We thus undertook the study of a larger cosmopolitan-based sample with widespread geographical origins. For that, we studied 200 unrelated white Brazilian males, originated primarily from large cities in the four main geographical regions of the country (north, northeast, southeast, and south).

The distribution of the AAI values for Brazil as a whole and for the four regions largely reproduced the previous results, albeit with some interesting regional differences (Fig. 4). The sample from the southeast, taken from the state of Minas Gerais, did not differ significantly from the rural sample of white individuals from the same state ($z = −1.26, P = 0.104$). This region also had the highest AAI median (−6.41). In contrast, the sample from south Brazil, the region with the highest levels of recent (19th and 20th centuries) European immigration, had a median AAI value of −9.11, 3 orders of magnitude smaller. However, when compared with the European (Portuguese) values, the southern sample still showed a significantly higher AAI values ($z = 3.04, P = 0.002$).

Admixture Estimation. From our results with the PSAs described by Parra *et al.* (11) we could calculate allele frequencies and use them to estimate the proportion of African admixture in the several samples studied (Table 2) by using two methods (16, 17). Although the standard errors of the estimates obtained with Long's method (18) are not small (Table 2) there is generally excellent agreement between the two estimates.

Discussion

Brazilians form one of the most heterogeneous populations in the world, which is the result of five centuries of interethnic crosses of peoples from three continents: the European colonizers, mainly represented by the Portuguese, the African slaves, and the autochthonous Amerindians. We have been studying this diversity systematically from a phylogeographical perspective. In our previous studies we used DNA lineage markers to ascertain
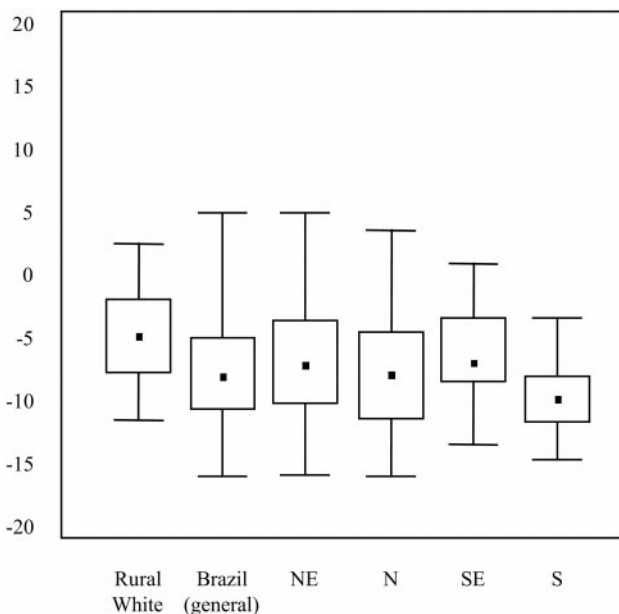
Fig. 4. Box plot graph showing the distribution of values of AAI in samples from Brazil (*n* = 200) and from the main regions of the country (NE = northeast, N = north, SE = southeast, and S = south). For comparison we included the data obtained from northern Portuguese and from the rural sample of white Brazilians already shown in Fig. 3. Each group is represented as a box whose top and bottom are drawn at the lower and upper quartiles, with a small square at the median. Thus, the box contains the middle half of the scores in the distribution. Vertical lines outside the box extend to the largest and the smallest observations within 1.5 interquartile ranges from the box (20).

the continental ancestry of Brazilian white individuals. Our data demonstrated that the vast majority of Y chromosomes in white Brazilian males, regardless of their regional source, were of European origin, with a very low frequency of sub-Saharan African Y chromosomes and a complete absence of Amerindian contributions (14). On the other hand, by analyzing mtDNA, we found the surprisingly high amount of 33% Amerindian and 28% African contribution to the total mtDNA pool of white Brazilians (23). Together, our results configured a picture of strong directional mating in Brazil involving European males and Amerindian and African females.

Because Brazil has a large territory and because different population groups moved into diverse parts of the country, there is considerable phylogeographical heterogeneity. When we an-

alyzed mtDNA in the four main regions of Brazil we found that there was broad agreement with what could be expected from historical data: a predominance of Amerindian matrilineages in the Amazon (north) region, a preponderance of African lineages in the northeast, an equilibrium in the southeast, and European dominance in the south (Table 2). There was relatively good concordance of the mitochondrial data with the estimates of African ancestry from the present study in Brazilian whites from the four main regions of Brazil. The most pronounced levels of admixture were observed in the southeast and the northeast, the former being slightly higher, although the difference is obviously not statistically significant. This finding is compatible with historical evidence that Minas Gerais (southeast) society was more admixed than the coastal sugar zone (northeast) (24), but contrasts with the higher proportion of African mtDNA lineages observed in the northeast than in the southeast (Table 2). Such discrepancy is probably related with the demographical peculiarities of the two regions. On the other hand, the south and the north have lower African admixture although they differ significantly in the relative proportions of European and Amerindian, i.e., non-African, mtDNA lineages. This observation highlights a methodological shortcoming in that the set of PSAs designed by Parra *et al*. (11) cannot (and was not meant to) discriminate between Europeans and Amerindians. Considering the trihybrid nature of the Brazilian population, it would be desirable to have specific markers that would allow the specific dissection of the Amerindian contribution. Although some authors (e.g., ref. 19) have identified markers that might be useful for this purpose, there are serious theoretical difficulties. As pointed out by Cavalli-Sforza *et al*. (25), the enormous amounts of genetic drift existent in many South American native groups has generated exceptional gene-frequency variation (reviewed in ref. 26) that severely weakens or renders invalid admixture inferences. Even if we averaged gene frequencies over extant populations, we could have no idea how these frequencies were in the past, when the admixture took place.

There was also excellent agreement between the two admixture estimates in the Queixadinha population for the three different Color categories. It is interesting to note that the group of individuals classified as blacks had a very high proportion of non-African ancestry (48%). Also, the intermediate group, with 45% African ancestry, was closer to the black group than to the white one. For the whole Queixadinha population, regardless of skin color, the admixture estimate was 0.44 ± 0.07.

Several attempts to estimate admixture in the Brazilian population were performed in the past, most of them using autosomal polymorphisms, especially blood groups and electrophoresis protein markers (reviewed in ref. 27). In different geographical regions, estimates of the African contribution to

Table 2. Values of AAI, admixture estimates obtained by two different methods from the frequencies of 10 PSAs and the proportion of African, European, and Amerindian mtDNA lineages in two samples of the Brazilian population

Sample		AAI Median	Admixture estimate		mtDNA ancestry*		
			Method 1[†]	Method 2[‡]	African	European	Amerindian
Rural population	Whites	−4.55	0.31 ± 0.09	0.32	NS	NS	NS
(Queixadinha)	Intermediate	−2.86	0.45 ± 0.07	0.48	NS	NS	NS
	Blacks	−1.25	0.51 ± 0.07	0.52	NS	NS	NS
Regions of Brazil	North	−7.24	0.23 ± 0.06	0.24	0.15	0.31	0.54
	Northeast	−6.56	0.29 ± 0.09	0.30	0.44	0.34	0.22
	Southeast	−6.41	0.32 ± 0.10	0.32	0.34	0.31	0.33
	South	−9.03	0.13 ± 0.08	0.17	0.12	0.66	0.22

NS, not studied.
*Alves-Silva *et al*. (23).
[†]Estimate ± SE (18).
[‡]Collins-Schramm *et al*. (19).

the urban population varied from 4% to 34% and those for Amerindian involvement ranged from 0% to 27% (27). For instance, in the northeast, Salzano (28) calculated for the population as a whole, 51% European, 36% African, and 13% Amerindian ancestries whereas in the north, Santos and Guerreiro (29) obtained 47% European, 12% African, and 41% Amerindian descent, and in the southernmost state of Rio Grande do Sul, Dornelles *et al.* (30) calculated 82% European, 7% African, and 11% Amerindian ancestries. Krieger *et al.* (31) studied a population of Brazilian northeastern origin living in São Paulo with blood groups and electrophoretic markers and showed that whites presented 18% of African and 12% of Amerindian genetic contribution and that blacks presented 28% of European and 5% of Amerindian genetic contribution (31). Of course, all of these Amerindian admixture estimates are subject to the caveat mentioned in the previous paragraph. At any rate, compared with these previous studies, our estimates showed higher levels of bidirectional admixture between Africans and non-Africans.

The focus of past admixture studies has been the population as a whole and not the individual (28). Because physical appearance is so often used for racial categorization and prejudice, we wanted to ascertain to what degree it was correlated with genomic African ancestry, which could be accomplished only at a personal level. The first sample studied was a group of 173 individuals from the Queixadinha rural community, in the state of Minas Gerais (southeast). Each individual was examined clinically and classified as white, black, or intermediate, on the basis of a multivariate evaluation that included skin pigmentation in the medial part of the arm, hair color and texture, and the shape of the nose and lips. This evaluation was, of course, subjective. Nevertheless we tried to make it more reliable by introducing the necessity of concordance by two independent examiners for classification in the categories white and black. Others have used more quantitative parameters such as skin reflectance spectrophotometry (e.g., ref. 32), but measuring only skin pigmentation fails to take into consideration the other qualities that contribute to the complex Color trait (4, 9). One of the peculiar features of social relations in Brazil is the large number of Color categories that are subjectively distinguished in a community. Harris and Kotak (8) elicited 40 Color terms from a sample of 100 people in a small fishing village in northeastern Brazil. Of course, most of these terms denoted Colors in between white and black, and in our study we lumped them in the intermediate category, thus considerably simplifying the classification procedure.

The second component of the study was the estimation of the personal genomic origin, which was based on a battery of 10 PSAs described by Parra *et al.* (11) and was summarized in the individual AAI. It might be considered risky to try to establish genomic African ancestry on the basis of only 10 alleles. However, as demonstrated in our study of 20 Portuguese and 20 African individuals, the AAI values performed extremely well at an individual level. The AAI values observed for the São Tomé sample ranged from 2.9 to 13.6, whereas for the Portuguese it ranged from -16.4 to -4.9. On the other hand, when we analyzed the individuals from Queixadinha, we observed large variances and very significant overlaps among the three Color categories (Fig. 2). Only nine of the 30 black individuals had values within the African range and eight (27%) had AAI values within the Portuguese range. On the other hand, only 16 of the 29 white individuals had values within the Portuguese range and none had AAI values within the African range. Moreover, 40 of the 114 intermediate individuals (35%) had AAI values in the Portuguese range and 15 (13%) had values within the African range. In other words, at the individual level, there was no chance of obtaining a reliable Color classification on the basis of the genomic analysis of 10 PSAs.

One of the loci tested in the PSA battery, *OCA2*, encodes a melanosome transmembrane protein (P protein) and may be

responsible for part of the normal human variation in pigmentation (6). Thus, its presence in the battery might introduce a bias by inflating the AAI values of black-skinned individuals and conversely deflating them in white individuals, independently of genomic ancestry. Thus, we recalculated the AAI values for the Queixadinha Color categories omitting the OCA2 results (data not shown). Indeed, this recalculation resulted in significant convergence of AAI values: the median for black individuals decreased from -0.87 to -1.90 and the median for white individuals increased from -4.55 to -2.62. After removal of OCA2, the difference between the Queixadinha white and black categories is no longer statistically significant in a two-tailed test ($z = 1.8$, $P = 0.07$). These results strengthen our conclusion that in Brazilians Color is poorly correlated with African ancestry.

We further confirmed our results by using a second sample composed of 200 unrelated white Brazilian males, who came from the four major geographic regions of the country. All regions showed AAI values intermediate between Europeans and Africans, even southern Brazil, a region predominantly peopled by European immigrants. In essence, our data indicate that, in Brazil as a whole, Color is a weak individual predictor of African ancestry.

If we consider some peculiarities of Brazilian history and social structure, we can construct a model to explain why Color should indeed be a poor predictor of African ancestry at an individual level. Most Africans have black skin, genetically determined by a very small number of genes that were evolutionarily selected (5, 6). Thus, if we have a social race identification system based primarily on phenotype, such as occurs in Brazil, we classify individuals on the basis of the presence of certain alleles at a small number of genes that have impact on the physical appearance, while ignoring all of the rest of the genome. Assortative mating based on Color, which has been shown by demographic studies to occur in Brazil (22, 33), will produce strong associations among the individual components of Color. Indeed, we detected the presence of such positive associations at highly significant levels in the Queixadinha population (data not shown). On the other hand, we expect that any initial admixture association between Color and the PSAs will inevitably decay over time. It is easy to see how this combination of social forces could produce a population with distinct Color groups and yet with similar levels of African ancestry. Let us take as an example, the historically common Brazilian mating of a white European male with a black African slave woman: the children with more physical African features would be considered black, whereas those with more European features would be considered white, even though they would have exactly the same proportion of African and European alleles. In the next generation, the light-skinned individuals would assortatively tend to marry other whites and conversely the darker individuals would marry blacks. The long-term tendency would then be for this pattern to produce a white group and a black group, which would, nonetheless, have a similar proportion of African ancestry.

Our study makes clear the hazards of equating color or race with geographical ancestry and using interchangeably terms such as white, Caucasian, and European on one hand, and black, Negro, or African on the other, as is often done in scientific and medical literature (34, 35).

1. Carter, S. L. (2002) *The Emperor of Ocean Park* (Knopf, New York).
2. American Anthropological Association (1998) *Am. Anthropol.* **100,** 712–713.
3. Templeton, A. R. (1998) *Am. Anthropol.* **100,** 632–650.
4. Telles, E. E. (2002) *Ethn. Racial Stud.* **25,** 415–441.
5. Deol, M. S. (1975) *Ann. Hum. Genet.* **38,** 501–503.
6. Sturm, R. A., Box, N. F. & Ramsay, M. (1998) *BioEssays* **20,** 712–721.
7. Clinton, W. J. (Jan. 14, 2001) *N.Y. Times,* Section 4, p. 17.
8. Harris, M. & Kotak, C. (1963) *Sociologia* **15,** 203–208.
9. Guimarães, A. S. A. (1996) in *Raça, Ciência e Sociedade*, eds. Maio, M. C. & Santos, R. V. (Fiocruz, Rio de Janeiro), pp. 143–157.
10. Schwartzman, S. (1999) *Novos Estudos CEBRAP* **55,** 83–96.
11. Parra, E. J., Marcini, A., Akey, J., Martinson, J., Batzer, M. A., Cooper, R., Forrester, T., Allison, D. B., Deka, R., Ferrel, R. E. & Shriver, M. D. (1998) *Am. J. Hum. Genet.* **63,** 1839–1851.
12. Shriver, M. D., Smith, M. W., Jin, L., Marcini, A., Akey, J. M., Deka, R. & Ferrel, R. E. (1997) *Am. J. Hum. Genet.* **60,** 957–964.
13. Thomas-Domenech, J. M. & Padilla-Bolivar, A. (1965) *Atlas das Raças Humanas* (Livro Íbero-Americano, Rio de Janeiro), pp. B1–B4.
14. Carvalho-Silva, D. R., Santos, F. R., Rocha, J. & Pena, S. D. J. (2001) *Am. J. Hum. Genet.* **68,** 281–286.
15. Tomás, G., Seco, L., Seixas, S., Faustino, P., Lavinha, J. & Rocha, J. (2002) *Hum. Biol.* **74,** 397–411.
16. Orita, M., Iwahana, H., Kanazawa, H., Hayashi, K. & Sekiya, T. (1989) *Proc. Natl. Acad. Sci. USA* **86,** 2766–2770.
17. Santos, F. R., Pena, S. D. J. & Epplen, J. T. (1993) *Hum. Genet.* **90,** 655–656.
18. Long, J. C. (1991) *Genetics* **127,** 417–428.
19. Collins-Schramm, H. E., Phillips, C. M., Operario, D. J., Lee, J. S., Weber, L. J., Hanson, R. L., Knowler, W. C., Cooper, R., Hongzhe, L. & Seldin, M. F. (2002) *Am. J. Hum. Genet.* **70,** 737–750.
20. Sokal, R. R. & Rohlf, F. J. (1995) *Biometry* (Freeman, New York), 3rd Ed., pp. 423–439.
21. Pritchard, J. K., Stephens, M. & Donnelly, P. (2000) *Genetics* **155,** 945–959.
22. Salzano, F. M. & Freire-Maia, N. (1970) *A Study of Brazilian Populations* (Wayne State Univ. Press, Detroit), pp. 54–58.
23. Alves-Silva, J., Santos, M. S., Guimarães, P. E., Ferreira, A. C. S., Bandelt, H.-J., Pena, S. D. J. & Prado, V. F. (2000) *Am. J. Hum. Genet.* **67,** 444–461.
24. Conniff, M. L. & Davis, T. J. (1994) *Africans in the Americas: A History of the Black Diaspora* (St. Martin's Press, New York).
25. Cavalli-Sforza, L. L., Menozzi, P. & Piazza, A. (1994) *The History and Geography of Human Genes* (Princeton Univ. Press, Princeton).
26. Salzano, F. M. (2002) *Ann. Acad. Bras. Ciencias* **74,** 223–263.
27. Sans, M. (2000) *Hum. Biol.* **72,** 155–177.
28. Salzano, F. M. (1997) *Interciência* **22,** 221–227.
29. Santos, S. E. B. & Guerreiro, J. F. (1995) *Braz. J. Genet.* 18, 311–315.
30. Dornelles, C. L., Callegari-Jacques, S. M., Robinson, W. M., Weimer, T. A., Franco, M. H. L. P., Hickmann, A. C., Geiger, C. J. & Salzamo, F. M. (1999) *Genet. Mol. Biol.* **22,** 151–161.
31. Krieger, H., Morton, N. E., Mi, M. P., Azevedo, E., Freire-Maia, A. & Yasuda, N. (1965) *Ann. Hum. Genet.* **29,** 113–125.
32. Harrison, A. G., Owen, J. J., Da Rocha, F. J. & Salzano, F. M. (1967) *Hum. Biol.* **39,** 21–31.
33. Petruccelli, J. L. (1999) in *CNPD I e II: Concurso Nacional de Monografias sobre População e Desenvolvimento* (Comissão Nacional de População e Desenvolvimento, Brasília, Brazil), pp. 1–20.
34. Brace, C. L. (1995) *J. Forens. Sci.* **40,** 171–175.
35. Schwartz, R. S. (2001) *N. Engl. J. Med.* **344,** 1392–1393.