Craniometric Similarities Within and Between Human Populations in Comparison with Neutral Genetic Data

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Abstract The statement that pairs of individuals from different populations are often more genetically similar than pairs from the same population is a widespread idea inside and outside the scientific community. Witherspoon et al. ["Genetic similarities within and between human populations," *Genetics* 176:351–359 (2007)] proposed an index called the dissimilarity fraction (ω) to access in a quantitative way the validity of this statement for genetic systems. Witherspoon demonstrated that, as the number of loci increases, ω decreases to a point where, when enough sampling is available, the statement is false. In this study, we applied the dissimilarity fraction to Howells's craniometric database to establish whether or not similar results are obtained for cranial morphological traits. Although in genetic studies thousands of loci are available, Howells's database provides no more than 55 metric traits, making the contribution of each variable important. To cope with this limitation, we developed a routine that takes this effect into consideration when calculating ω. Contrary to what was observed for the genetic data, our results show that cranial morphology asymptotically approaches a mean ω of 0.3 and therefore supports the initial statement—that is, that individuals from the same geographic region do not form clear and discrete clusters—further questioning the idea of the existence of discrete biological clusters in the human species. Finally, by assuming that cranial morphology is under an additive polygenetic model, we can say that the population history signal of human craniometric traits presents the same resolution as a neutral genetic system dependent on no more than 20 loci.

Cranial morphology is widely used to assess biological affinities among extinct and extant human populations because of its clear pattern of geographic organization (Hanihara 1996, 1997; Hanihara et al. 2003; Harding 1990; Howells 1973, 1989, 1995; Manica et al. 2007; Neves and Hubbe 2005; Relethford 1994, 2002). However, despite its wide use, basic questions regarding the origin of cranial

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morphological variation in modern humans and the processes behind it remain unsolved. For example, despite the ever growing consensus in the literature that cranial morphology is a result of microevolutionary processes and environmental plasticity, the relative weights of these forces in the morphological development of the human skull are still uncertain. Although some investigators have questioned the use of cranial morphology to infer phylogeny (Carlson and Van Gerven 1977; Collard and Wood 2000; Larsen 1997), studies involving large geographic areas and numerous samples have successfully shown that cranial morphology closely resembles what is observed in neutral genetic markers (Harvati and Weaver 2006; Manica et al. 2007; Perez et al. 2007; Relethford 1994, 2002, 2004a, 2004b; Roseman 2004).

The close relationship between morphological and neutral genetic variation was first suggested by studies that demonstrated that craniometric traits, like many other phenotypic traits, have average moderate heritability (Carson 2006; Devor 1987; Konigsberg and Ousley 1995; Lynch and Walsh 1998; Martínez-Abadías et al. 2009; Mousseau and Roff 1987; Raposo do Amaral et al. 1989; Sherwood et al. 2008; Sparks and Jantz 2002), even though the heritability of each craniometric trait can vary considerably (Carson 2006; Martínez-Abadías et al. 2009). Under this assumption, genetic information could be retrieved from phenotypic traits, which were determined, at least partly, by quantitative genetic loci (Cheverud 1988). This first approach allowed certain population genetic concepts to be applied to cranial morphology (Roseman 2004; Sherwood et al. 2008; Varela and Cocilovo 2006). Statistics such as F_{ST} (Konigsberg 1990; Relethford and Blangero 1990; Relethford and Harpending 1994; Relethford et al. 1997; Williams-Blangero and Blangero 1989, 1990) and other means of inferring the influence of natural selection and/or stochastic evolutionary processes on cranial morphology (Ackermann and Cheverud 2004) significantly improved the possibility of exploring the structure of morphological variability on a global scale, allowing its comparison with neutral genetic markers.

For instance, Relethford (1994, 2002) demonstrated that the global variation apportionment of the human skull is similar to findings using neutral genetic markers (e.g., Barbujani et al. 1997; Bowcock et al. 1991; Lewontin 1972; Rosenberg et al. 2002), with only about 15% of total worldwide variation being a consequence of between-group differences. Manica et al. (2007) were able to show that morphological variability decreases according to distance from Africa, similar to what has been observed for neutral genetic markers (Cavalli-Sforza et al. 1994; Linz et al. 2007; Liu et al. 2006; Manica et al. 2005; Prugnolle et al. 2005; Ramachandran et al. 2005; Serre and Pääbo 2004), supporting a single origin for modern humans. Martínez-Abadías et al. (2006) also emphasized the genetic background of cranial morphology by demonstrating that the hybrid offspring of two different populations present, at least to some extent, an intermediate cranial morphology, suggesting that such phenotypic traces can be considered to be mainly under the control of an additive polygenetic system.

However, all evidence favoring a neutral evolutionary basis for the cranial morphological diversity of modern human groups seems to hold only when cranial morphology is analyzed as a whole and across wide geographic areas. In more localized studies, environmental plasticity has been suggested to play a more relevant role in morphological differentiation (Relethford 2004a). Specific studies have suggested that some craniometric measurements and anatomical regions might be under the influence of long-term selection in response to climate conditions, especially when populations adapted to extremely cold conditions are considered (Beals et al. 1984; Bernal et al. 2006; Harvati and Weaver 2006; Hubbe et al. 2009; Roseman 2004; Roseman and Weaver 2004). Significant correlations between specific craniometric measurements and environmental factors, such as altitude (Guglielmino-Matessi et al. 1979; Rothhammer and Silva 1990) and lifestyle (Carlson and Van Gerven 1977; González-José et al. 2005; but see Paschetta et al. 2010), have also been described. These correlations have been used by some to argue in favor of a high morphological response of skull shape to local environmental conditions.

Thus cranial morphology has been shown to be a complex entity under the influence of a vast array of differentiation processes affecting distinctly different anatomical regions. And, as such, the fundamental issue remains the same: To what extent does human cranial morphology reflect the ancestor-descendant relationships of different human populations compared to neutral molecular markers (Rosenberg et al. 2003)? Or, in other words, what is the nature of the relationship between molecular and morphological markers (Merilä and Crnokrak 2001; Roseman and Weaver 2007)?

The structure of morphological variation and its apportionment within or between populations has been a relevant issue of discussion in the last 15 years, especially in relation to the discussion of the existence of human races. It has been recurrently stated for neutral molecular data that, because most of the variation seen in modern human groups can be found within groups and not between groups, discriminatory power between human populations is limited, and the concept of human races cannot be sustained [Lewontin 1972; Relethford 1994, 2002; but see Edwards (2003) for a critical view]. In other words, as originally stated by the American Anthropological Association (1997: 1), because of the intrinsic organization of modern human biological variation, it is expected that *any two individuals within a particular population are as different genetically as any two people selected from any two populations in the world* (Bamshad et al. 2004; Steele 2002; Witherspoon et al. 2007).

This statement has received positive empirical support from Bamshad et al. (2004), who, using 377 STRs, found that roughly one-third of the individuals from the same continent were more different than individuals from different continents. However, Witherspoon et al. (2007) were able to refute this claim through the calculation of a dissimilarity fraction (ω) for neutral molecular markers, an index especially designed to address this matter. Simply put, the dissimilarity fraction represents the proportion of pairs of individuals from the same population that

Table 1. Craniometric Measurements Used in This Study

Variable[a]	*Variable*[a]	*Variable*[a]
Alveolar radius	Frontal subtense	Nasion-subtense fraction
Basion-bregma height	Frontal malare radius	Nasio-occipital length
Basion-nasion length	Glabella subtense	Occipital cord
Basion-prosthion length	Glabello-occipital length	Occipital subtense
Biasterionic breadth	Interorbital breadth	Orbit breadth
Biauricular breadth	Lambda-subtense fraction	Orbit height
Bifrontal breadth	Malar length, maximum	Palate breadth, external
Bijugal breadth	Malar length, inferior	Parietal cord
Bimaxillary breadth	Malar subtense	Parietal subtense
Biorbital breadth	Mastoid breadth	Prosthion radius
Bistephanic breadth	Mastoid height	Simotic cord
Bizygomatic breadth	Maximum cranial breadth	Subspinale radius
Bregma-subtense fraction	Maximum frontal breadth	Supraorbital projection
Cheek height	Minimum cranial breadth	Vertex radius
Dacryon radius	Nasal breadth	Zygomaxillare radius
Dacryon subtense	Nasal height	Zygomaxillary subtense
Ectoconchion radius	Nasio-frontal subtense	Zygo-orbitale radius
Foramen magnum length	Nasion-prosthion height	
Frontal cord	Nasion radius	

a. Nomenclature and definitions according to Howells (1973, 1989).

is genetically more different than pairs sampled from different populations. As demonstrated by Witherspoon and co-workers, ω declines with the increase in the number of loci included in the analysis, reaching 0 when approximately 800 loci are studied. In other words, when more than 800 loci are considered, no pair of individuals from the same population is more different than any pair of individuals from any two populations.

The goal of this study is to extend the calculation of ω to craniometric data, under the assumption that craniometric traits, being largely influenced by stochastic microevolutionary processes, will present the same behavior observed by Witherspoon et al. (2007) for genetic loci—that is, that the dissimilarity fraction has an inverse relationship with the number of variables used in its computation, reaching a null value when enough information is provided.

Materials and Methods

The craniometric data used in this study are 55 linear measurements of the skull (see Table 1) from Howells's database (Howells 1973, 1989, 1995). Following the criteria adopted by Witherspoon et al. (2007), we selected nine series, representing three major geographic areas (Africa, East Asia, and Europe) (Table 2). The same three regions were selected by Witherspoon et al. (2007) in an attempt to ensure that the global genetic variability would be included in their study. We chose similar regions to allow for direct comparison between the results obtained

Table 2. Samples Included in This Study

Region and Local Population	*Male Sample Size*	*Female Sample Size*
Africa		
Dogon	47	52
Teita	33	50
Zulu	55	46
Asia		
Hainan	45	38
North Japan	55	32
South Japan	50	41
Europe		
Berg	56	53
Norse	55	55
Zalavar	53	45

a. All data are from Howells (1973, 1989).

here and those presented for molecular data by Witherspoon and co-workers. Males and females were analyzed separately to reduce the effects of allometry and sexual dimorphism. The data were not submitted to any statistical correction or size adjustment procedure.

As detailed by Witherspoon et al. (2007), the dissimilarity fraction ω is the probability that a pair of individuals randomly chosen from different populations will be more similar to each other than an independent pair of individuals of one population. To obtain ω, distances between all pairs of individuals are calculated and classified as within or between populations. Next, the value of ω is estimated as the frequency of the times that the within-population distance is larger than the between-population distance. The dissimilarity fraction ranges from 0 to 0.5, because when two populations are identical there is an equal probability that individuals from one population will be more similar or more different than individuals from distinct populations.

The advantage of the dissimilarity fraction over other discriminant procedures—and the reason that we adopted it here—is that it does not assume a priori the existence of group centroids or biological central tendencies for each group. As such, the calculation of ω is not influenced by either this central tendency or the assumed variance or covariance that results from it. The practical consequence of this for the discussion of the structure of morphological (or biological) diversity is that, because ω is not a typical discrimination procedure, it does not force the existence of discrete clusters, focusing rather on the direct relationship among the individuals of different populations.

Genetic data offer the possibility of obtaining thousands of variables in the form of different loci to use in the calculation of ω. Under this condition, the effect of each single variable (locus) and of the loci's covariance is almost negligible, and the exchange of one locus for another does not significantly alter the value of

ω. Craniometric data, on the other hand, are limited to a small number of variables (55 in this case), and covariance between them is usually moderate to high. As a consequence, different sets of cranial measurements can result in distinct values of ω.

Because we are interested in evaluating the mean effect of the increase of variable numbers in the value of ω, we decided to use a computational routine that computes the values of ω 1,000 times with a randomly chosen array of n variables (without replacement), where n is the number of variables included in the calculation of ω. For example, to establish the value of ω using 30 variables, the routine computes ω 1,000 times with different arrays of 30 randomly chosen variables. The dissimilarity fraction is calculated as the mean value for all permutations, and its 95% confidence limits are given by ±1.96 times their standard deviation. Euclidean distances were used to build up the distance matrix used to compute the value of ω. Although Euclidean distances do not weight the contribution of each variable according to its covariance to other variables (as would occur in other commonly used distances for morphologic data; Mahalanobis 1936), we chose this distance because of the impracticability in terms of computational time of running the permutations with more complex distances. However, because this study is based on 1,000 randomly selected sets of variables for each number of variables selected, it is reasonable to assume that the effects of the covariance between the craniometric measurements are equally considered, independent of the number of variables used to calculate ω. As a result, the comparisons of ω between the different numbers of variables selected for its calculation should not be affected by distinct covariance levels between the variables selected in each case.

The analysis was performed twice: once on a continental level (i.e., individuals were classified according to their continents) and again on a population level (i.e., individuals were classified according to their local population for each continent). These different approaches allowed us to evaluate the effect of comparing isolated populations against more closely related ones. All calculations were performed with a routine written by one of us (A. Strauss) in C language; the program is available upon request.

Results

Figure 1 shows the mean values and the 95% confidence interval of ω for males according to the increasing number of variables used in the calculation of ω. When the series are pooled according to large geographic areas (continents), the mean value of ω starts with 0.43 for 5 variables and decreases as the number of variables is increased until stabilizing at about 0.36 when 55 variables are used (Figure 1a). For the three analyses where the series are separated according to local populations (Figures 1b–d), the same pattern is observed. The Asian samples present the highest values of ω, ranging from 0.48 for 5 variables to 0.46 for the complete set of measurements. Africans show the lowest values of ω and Europeans show intermediate values, ranging from 0.43 (Africans) and 0.46 (Europeans)

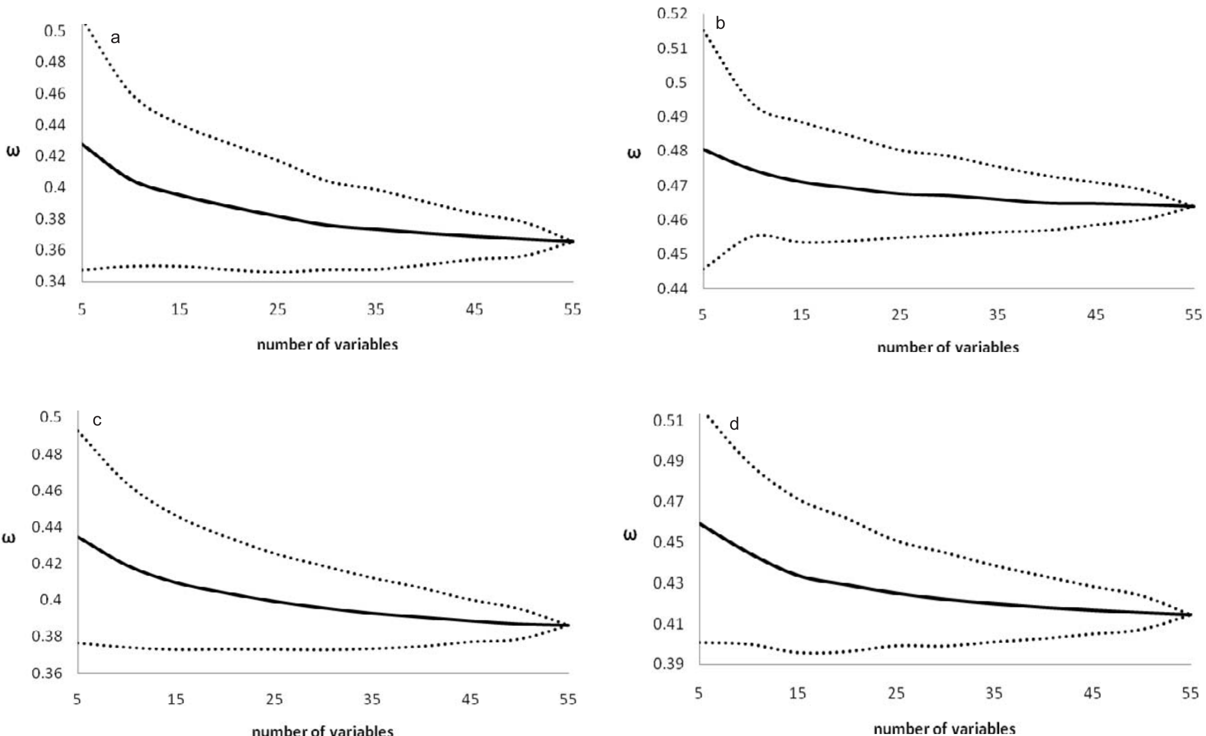

Figure 1. Dissimilarity fraction of males according to the increasing number of variables in the model. Solid lines are the mean values of ω, and dotted lines delimit the ±95% confidence interval obtained after 1,000 iterations. (a) Series pooled according to large geographic areas (continents). (b) Asian series pooled according to their local populations. (c) African series pooled according to their local populations. (d) European series pooled according to their local populations.

for 5 variables to 0.39 (Africans) and 0.41 (Europeans) for the complete set of measurements. These three analyses consistently present higher values of ω than those obtained on a continental scale.

When females are considered, the results are similar (Figure 2). The mean value of ω ranges from 0.44 for 5 variables to 0.38 when 55 variables are used (Figure 2a). Similar results are seen for the within-region analysis (Figures 2b–d) with the only difference being that Africans present a lower ω than the sample organized by continents. Also, the hierarchy of ω for each region is the same as that observed for males: Asia presents the highest values (0.48–0.46), and Africans show the lowest values (0.43–0.36) and Europeans show intermediate values (0.46–0.40).

Discussion

The most reliable alternative to infer ancestor-descendant relationships among human populations is neutral genetic markers. Yet neutral molecular markers are not always readily available to infer microevolutionary processes among extinct and extant human populations, and thus cranial morphology has been commonly used to this end (e.g., Hanihara 1996; Howells 1973, 1989, 1995; Neves and Hubbe 2005; among many others).

Although cranial morphology has been challenged as a tool to infer population history (Collard and Wood 2000), several works in the last 15 years have demonstrated that the morphological variation seen among modern humans is geographically structured, and most of this variation can be explained by isolation-by-distance processes of differentiation (Harvati and Weaver 2006; Relethford 2004b, 2008; Roseman 2004).

In general terms, these studies followed the pioneering approach of Relethford (1994, 2002), who suggested that the human skull evolved mainly through genetic drift. Relethford also demonstrated that the apportionment of morphological and genetic variability was the same within and among human populations (i.e., $F_{ST} \cong 0.15$). However, the importance and the real significance of F_{ST} in understanding the partitioning of global diversity have been severely questioned in the last decade. Long and Kittles (2003) stressed that F_{ST} estimates may neglect relevant aspects of human genetic diversity, allowing for important genetic differences to pass unseen. Edwards (2003) made a similar claim, according to which F_{ST} is not well suited for the study of human genetic diversity because it does not consider the correlations between different variables [but see Neigel (2002)].

This means that the current assumption that the population structure of human cranial morphology and neutral molecular markers are similar must be viewed with caution. Our results favor this idea by showing that important differences are observed between craniometric and genetic data when the variation structure is considered from the perspective of the similarities within and between human individuals, despite the fact that the dissimilarity fraction decreases with an increasing number of variables for both types of markers (Witherspoon et al. 2007). Although for the

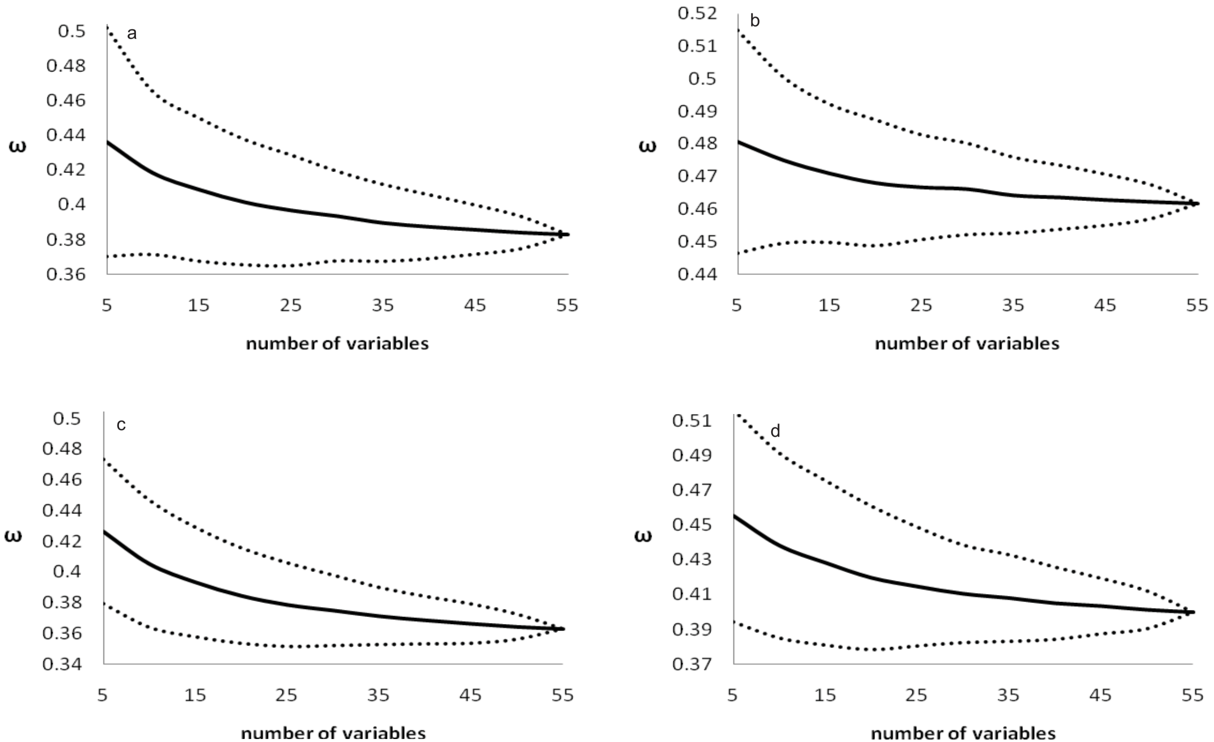

Figure 2. Dissimilarity fraction of females according to the increasing number of variables in the model. Solid lines are the mean values of ω, and dotted lines delimit the ±95% confidence interval obtained after 1,000 iterations. (a) Series pooled according to large geographic areas (continents). (b) Asian series pooled according to their local populations. (c) African series pooled according to their local populations. (d) European series pooled according to their local populations.

molecular data ω reaches 0 when sufficient information is provided, the craniometric ω is not even close to null when all available variables are used.

The results for phenotypic data indicate that when all morphological information is used to compute the dissimilarity fraction, this index does not even reach 0.35 as its smallest value. Considering that the maximum value for ω is 0.50, the dissimilarity fraction for human cranial morphology is considerably high and supports the statement that two individuals of the same population are often more different than two individuals from different populations, in contrast to what is observed with neutral molecular markers when enough loci are used in the analysis (Witherspoon et al. 2007). However, even the null ω values obtained by Witherspoon et al. (2007) must be viewed with some caution, because these investigators based their analysis on populations far apart from each other (i.e., Africa, East Asia, and Europe). When more closely related populations are considered, the differentiation among populations is considerably harder to achieve, if it is possible at all [see Witherspoon et al. (2007) and Jakobsson et al. (2008) for examples]. In this sense, the high values of ω obtained for the craniometric data are even more remarkable, because our analyses were also based on populations from distant geographic regions and a higher degree of differentiation among them should be expected.

Yet the observed differences between morphological and molecular data are by no means unexpected. Although it is true that neither molecular markers nor craniometric traits are completely independent entities, the morphological integration behind the skull architecture (Bastir et al. 2006; Cheverud 1982; Enlow 1990; González-José et al. 2004; Lieberman et al. 2000; Moss and Young 1960; Sperber 1989) probably implies high levels of pleiotropy. This certainly constrains the rate of morphological evolution compared to noncoding molecular markers. Genetic and morphological evolution are not two completely separate entities in human evolution, but the differences observed between them in this study support the notion that human biological variation is discordant among distinct traits. Specifically in this case, under the assumption that cranial morphology does reflect phylogenetic relationships among human groups, as argued before, our results suggest that among-regions morphological diversity can hardly be said to be organized in discrete clusters.

As indicated by the high standard deviations obtained in our analyses, each craniometric trait has a distinct effect on ω. Such behavior is expected and reflects the fact that cranial morphology is composed of relatively independent functional regions (Bastir et al. 2006; Bookstein et al. 2003; Enlow 1990; González-José et al. 2004; Lieberman et al. 2000; Marroig et al. 2009; Moss and Young 1960; Oliveira et al. 2009; Porto et al. 2009; Sperber 1989), which might be responding distinctly to different evolutionary pressures. For instance, craniometric dimensions influenced by diversifying selection, such as certain facial and neurocranial breadth dimensions (Harvati and Weaver 2006; Hubbe et al. 2009; Roseman 2004), would result in a stronger reduction of ω than variables that mainly reflect processes of differentiation resulting from isolation by distance.

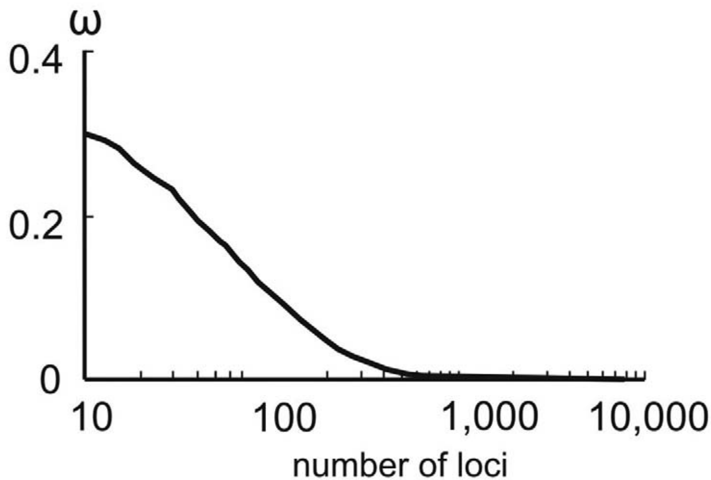

Figure 3. Dissimilarity fraction plotted against number of loci used in its computation. The populations used to compute ω were from Africa, Europe, and East Asia, and the molecular data are from SNP microarrays. The *x* axis is a logarithmic scale because of the high number of loci available for this analysis; direct comparison of this figure with Figures 1 and 2 must take this into account. Adapted after Witherspoon et al. (2007).

It is important to consider that the morphological information used in this study is limited to the metric traits traditionally used by Howells (1973, 1989). The base of the skull, for example, is underrepresented in this data set, although it has been defended as the most genetically determined and evolutionarily conservative anatomical region of the cranium (Olson 1981; Wood and Lieberman 2001). Increasing the number of anatomical regions and metric traits in the analyses would probably improve the degree of differentiation among populations. Still, the subasymptotic behavior of the ω curves indicates that craniometric measurements become highly redundant when more than 30 variables are included in the analyses.

The degree of redundancy in the information added by each craniometric variable is better observed when craniometric data are directly compared to the molecular results. For a phenotypic trait determined by an additive polygenetic system with no dominance, genotypic patterns would be extended to phenotypic ones. From Figure 3, redrawn after Witherspoon et al. (2007: 356), it is possible to ascertain, for example, that a trait determined by 40 loci would yield a dissimilarity fraction of about 0.2. Inversely, it would be expected that a hypothetical phenotypic entity that presents a dissimilarity fraction of 0.2 would be determined by 40 additive loci of equal effect. When this logic is applied to our results (Figures 1a and 2a), the prediction is that no more than 20 additive loci would influence cranial morphology variation when all variables are considered together.

Although we are certainly not suggesting that this is indeed the case, the fact that differentiation between human populations based on the skull presents the same resolution (i.e., the same value of ω) of a genetic system of no more than 20 SNPs demonstrates that caution must be taken when inferences about the structuring of human genetic diversity are made on the basis of craniometric data.

The high dissimilarity fraction values reported here and the general low F_{ST} values reported for morphological data (Relethford 1994, 2002) might be seen as contradicting previous studies (Howells 1973; Hubbe and Neves 2007; Relethford 2009; among others) that demonstrated high correct classification rates of individuals to their original population according to discriminant functions (as a matter of fact, for Howells's series, correct classifications range from 75% to 98%, depending on the geographic region; Hubbe and Neves 2007). However, as mentioned before ("Materials and Methods" section) classificatory analyses achieve high levels of success because they depend on the a priori definition of group centroids. As a consequence, when a large number of variables is considered, the probability that this kind of analysis will find a dimension in the original data that differentiates among the a priori defined groups is high. Yet the precise biological significance of this kind of difference is hard to establish, especially when the high values of dissimilarity fractions reported here are considered. High rates of correct discrimination of groups can thus be misleading in understanding the structure of human biological diversity.

Our results also have implications for the discussion about the existence of races in the human species from the phenotypic point of view because they support the notion of an absence of discrete biological groups. Despite the geographic structuring of morphological variation previously reported in other studies and the influence of diversifying selection associated with cold climate in some craniofacial dimensions, the results presented here demonstrate that roughly one-third of the pairs of individuals within a population are more different than pairs of individuals between populations. This indicates that cranial morphology is less able to identify nonclinal variations among populations (which would be in accordance with the existence of biological races in the human species) than molecular data are, which, in contrast to cranial traits, can show null dissimilarity fractions if enough loci are considered.

Conclusion

The results presented here for the dissimilarity fraction of human craniometric traits are in disagreement with the results obtained for molecular data. The high dissimilarity fraction that we obtained using a data set that has been shown to have a strong geographic organization (Howells 1973, 1989) demonstrates that this organization is less structured than previously thought. To be more precise, when an index not designed to accentuate differences between groups is used, the contrast in skull shape between three major regions of the globe (Europe, Asia, and Africa) becomes ephemeral.

Also, under the assumption, widely supported in the last decades, that cranial morphology does reflect population history as much as neutral molecular markers do (Harvati and Weaver 2006; Hubbe et al. 2009; Manica et al. 2007; Relethford 1994;), this study supports the notion that human biological variation is discordant among distinct categories of traits. This demonstration that human diversity is not always consistent across traits (molecular × morphology in this case) shows that studies about worldwide human biological diversity should consider distinct sources of information before drawing conclusions on the nature of its organization.

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