Quantifying Variation in Human Scalp Hair Fiber Shape and Pigmentation

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ABSTRACT

Objectives: This study aims to evaluate the use of quantitative methods of measuring variation in scalp hair fiber shape and pigmentation and carry out exploratory data analysis on a limited sample of individuals from diverse populations in order to inform future avenues of research for the evolution of modern human hair variation.

Methods: Cross-sectional area and shape and average curvature of scalp hair fibers were quantified using ImageJ. Pigmentation was analyzed using chemical methods estimating total melanin content through spectrophotometric methods, and eumelanin and pheomelanin content through HLPC analysis of melanin-specific degradation products.

Results: The initial results reinforced findings from earlier, traditional studies. African and African Diaspora scalp hair was significantly curled, (East) Asian hair was significantly thick, and European hair was significantly lighter in color. However, pigmentation analyses revealed a high level of variability in the melanin content of non-European populations and analysis of curvature found a large range of variation in the average curvature of East African individuals.

Conclusions: Overall, these results suggest the usefulness of chemical methods for the elucidation of nonperceptible differences in scalp hair color and highlight the need for improvements in our assessment and understanding of hair fiber curvature. Am J Phys Anthropol 160:341–352, 2016. © 2016 Wiley Periodicals, Inc.

Humans are among the few mammals that lack the full coat of fur characteristic of the class Mammalia. Moreover, *Homo sapiens* has uniquely retained a covering of thick terminal hair on the scalp. Intriguingly, while scalp hair is a universal human trait, it exhibits a wide range of variation in fiber shape and color (Trotter, 1938; Hrdy, 1973; Loussouarn et al., 2007; Ito and Wakamatsu, 2011). Yet the evolutionary basis for human hair diversity remains largely unexplained. Within the context of "racial" variation among populations, Darwin (1877) developed his theory of sexual selection as an explanation for variation in superficial traits such as hair color, skin color, and facial structure. Since Darwin, a number of hypotheses have been put forth to explain particular variants of scalp hair. With regards to the tightly curled hair found in many African populations, thermoregulation has been implicated as a possible selective pressure (Jablonski, 2006; Robbins, 2012). The reasoning behind this is that curled African hair fibers form a sparse structure on the head, allowing air to pass through and cool the scalp (Jablonski, 2006, p 50). Blond coloring of hair has been hypothesized to have arisen due to strong sexual selection for the trait, specifically in females, during the Upper Paleolithic in Europe (Frost, 2006). However, neutral genetic processes may also have had an important part to play in the evolution of human hair variation. For example, the high frequency of blond hair among Melanesians has been attributed to founder effect in the *TYRP1* mutation (Kenny et al., 2012; Norton et al., 2014), thus illustrating the importance of exploring mechanisms other than selection when considering the evolution of human hair diversity.

Though hair fiber curvature is a continuous trait, it is often still described categorically (e.g., Medland et al., 2009). In 2007, Loussouarn and coworkers published a study on the "worldwide diversity of hair curliness" using a sample of over 2000 individuals from around the world. The continuous curvature metrics used in their study (described in De La Mettrie et al., 2007) are derived from Hrdy's original assessment of variation in hair form (Hrdy, 1973; De La Mettrie et al., 2007; Loussouarn et al., 2007) and Bailey and Schliebe (1985). However, Loussouarn and coworkers ultimately use these various continuous measures of hair curvature to develop a classificatory system for hair curliness. Aside from the work of Hrdy (1973), De La

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Mettrie et al. (2007) and Loussouarn et al. (2007), there have been few studies of global variation in hair fiber shape, and the trait has not been adequately considered in an evolutionary context. Hair fiber cross-sectional geometry, by comparison, has been more thoroughly studied, with numerous publications revealing quantitative differences between populations (Vernall, 1961; Hrdy, 1973; Hutchinson and Thompson, 1997; Franbourg et al., 2003; Swift, 2006; Mou et al., 2008). With regard to hair fiber thickness in particular, recent genetic studies have demonstrated strong signals of selection in East Asian populations for a mutation in the *EDAR* locus associated with thicker hair (Fujimoto et al., 2008a).

There have been a number of recent publications on the genetic background of hair color variation in Europeans and Melanesians (Graf et al., 2005; Sulem et al., 2007; Branicki et al., 2008; Sturm, 2009; Kenny et al., 2012; Norton et al., 2015a,b), but none on the distribution of hair pigmentation around the world. The identification of phenotypes for some genetic studies is based on categorical descriptions of hair color (e.g., Flanagan et al., 2000; Branicki et al., 2008), which may lack the accuracy necessary for revealing relevant genes in non-European populations (Norton et al., 2015a). Reflectance spectrophotometry, as a quantitative method of assessing hair pigmentation, has been applied to a number of genetic studies on hair color variation, successfully demonstrating the contribution of *OCA2*/*HERC2* and *IRF4* to European variation in hair pigmentation (Norton et al., 2006, 2015a; Shekar et al., 2008a,b; Candille et al., 2012). The quantification of hair pigmentation in these studies involved the use of a spectrophotometer to measure the reflectance of hair either directly from the scalp (Norton et al., 2006, 2015a) or from a hair sample that has been cut (Shekar et al., 2008a,b). While the use of spectrophotometers appears to be successful for detecting the range of variation displayed by European individuals, the use of even more fine-scale quantitative methods might be warranted for the assessment of non-European hair pigmentation variation (Norton et al., 2015a). It is possible to estimate the total melanin (TM) content of a small sample of solubilized hair through spectrophotometric analysis (Ozeki et al., 1996; Commo et al., 2012). Alternatively, high-performance liquid chromatography (HPLC) can be used to analyze specific degradation products of pheomelanin (PM) and eumelanin (EM) to estimate their content in a hair sample (Wakamatsu et al., 2002; Ito et al., 2011). These last two methods, though relatively more time-consuming and costly than the use of spectrophotometers, may represent a way to reveal any potential fine-scale variation in the hair pigmentation of non-European populations.

In this study, we present the results of our quantitative assessments of scalp hair fiber curvature, cross-sectional geometry, and pigmentation on a limited sample of individuals with diverse bio-geographical ancestry and carry out exploratory data analysis in an attempt to inform possible future avenues of research for the testing of evolutionary hypotheses using quantitative hair fiber shape and pigmentation data.

MATERIALS AND METHODS

Samples

A total of 79 individuals were recruited in the United Kingdom through Cambridge University, King's College London, London School of Economics and a social media appeal for the purposes of this study (see Table 1). Following the provision of signed consent, participants completed a questionnaire focused on history of hair treatments and genealogic ancestry (see Supporting Information Document 1). A lock of scalp hair, $\leq$5 mm in breadth and $\geq$20 mm in length, was cut from the occipital region at a maximum of 10 mm from the root. After collection, all samples were washed once using a solution of water and shampoo (Boots Essentials Shampoo, The Boots Company PLC, Nottingham, UK), rinsed twice, and air-dried overnight prior to analyses. This study received ethical approval from the School of Humanities and Social Sciences Research Ethics Committee, University of Cambridge.

Participant ancestry and population designation

In the absence of genetic data, ancestry was established through detailed genealogical ancestry self-report. The questionnaire asked participants to indicate their own birthplace and ethnic identity as well as that of their grandparents (Supporting Information Document 1). This allowed individuals to be grouped into geographically defined "populations" based on regional classifications defined by the United Nations Statistics Division (2013) (details on population designation are available in Supporting Information Table 1). Due to the small sample size, and to facilitate the visualization of trends, regional populations were aggregated into larger regional groups: "African," "European," "Asian," and "African Diaspora" with a number of participants of mixed ancestry categorized as "Mixed Individual" (Table 1).

Cross-sectional geometry analysis

Samples were suspended taut between two pieces of cardboard (spaced at 2–3 cm) and impregnated in a clear resin. Once the resin hardened, it was cut at an angle perpendicular to the long axis of the hair to create slides ($\sim$10 $\times$ 4 $\times$ 1.5 cm in size) for microscopic analysis. All slides were polished using silicon carbide paper to improve visibility (grit sizes P240-P2500). A cross-sectional image of each hair was captured at a resolution of 600DPI (23.622 pixels/mm) using a camera-equipped stereoscopic microscope (Leica M205 C) and three hairs were analyzed per person. Images were imported into ImageJ and measured for maximum and minimum diameter. Cross-sectional area was calculated using the formula for elliptic area: πab, where a represents the minimum radius of the ellipse and b represents the maximum radius of the ellipse. Cross-sectional shape was calculated as the maximum diameter divided by the minimum diameter: more circular cross-sectional shapes are represented by numbers closer to 1.0, and more elliptical shapes are represented by values further from 1.0.

Curvature analysis

Single strands of hair were placed on a sheet of blank white paper, the application of mechanical stress was avoided to ensure unaltered curvature, and the paper was covered with a transparent sheet of acetate to facilitate a two-dimensional measurement. Three hairs were analyzed per person in order to provide a representative average for each individual. Samples were scanned using a flatbed scanner (CanoScan LiDE 600F) at a resolution of 1200 DPI. Curvature measurements were collected in ImageJ version 1.48. Each curve in a hair fiber was traced digitally, creating a separate data point from each curve.

TABLE 1. Breakdown of samples by population and sex

Group	Age (SD)	Population	Sex: Male	Sex: Female	Total
African ($n = 21$)	21.0 (9.5)	Western Africa	1	6	7
		Eastern Africa	6	4	10
		Northern Africa	0	1	1
		Southern Africa	0	1	1
		Central Africa	1	1	2
			8	13	21
European ($n = 18$)	20.6 (1.3)	Western Europe	0	2	2
		Eastern Europe	3	1	4
		Northern Europe	6	4	10
		Southern Europe	2	0	2
			11	7	18
Asian ($n = 13$)	20.9 (1.4)	Eastern Asia	6	0	6
		Southern Asia	3	3	6
		Mixed Asian	1	0	1
			10	3	13
African Diaspora ($n = 20$)	27.0 (8.7)	Caribbean	1	18	19
		African American	0	1	1
			1	19	20
Mixed Individuals ($n = 7$)	23.0 (4.6)	Mixed European/Caribbean	0	3	3
		Mixed European/African	1	2	3
		Mixed European/ African/Caribbean	1	0	1
			2	5	7

Curvature varied greatly among individuals, thus the number of measurements per hair varied from as few as two to as many as 60 (Fig. 1). The mean, maximum, and minimum curve diameters from a single hair are then computed. Curvature is the inverse of the radius (curve diameter ÷ 2), so the previously computed values yield a mean, maximum, and minimum curvature. The variable average curvature is the mean curvature averaged from the three hairs analyzed for a single individual. The variable irregularity is similarly calculated as an individual's averaged maximum to minimum curvature ratio. Both average curvature and irregularity variables are derived from Hrdy (1973). Precise instructions for the method of curvature analysis described in this study have been made available (Supporting Information Document 2) and a depiction of the application of this digital method can be seen in Figure 1.

Pigmentation analysis

After being washed and dried, a portion of the hair sample collected from each participant was analyzed at the Department of Chemistry, Fujita Health University School of Health Sciences, Japan using previously published techniques (Ito et al. 2011). In brief, hair samples (~1.0 mg) were subjected to Soluene-350 solubilization and analyzed for absorbance at 500 nm, values for which were multiplied by a factor of 101 to convert to the TM value (Ozeki et al., 1996). Values for EM and PM were based on HPLC analysis of the degradation products pyrrole-2,3,5-tricarboxylic acid, following alkaline hydrogen peroxide oxidation, as a marker of EM (Ito et al., 2011) and 4-amino-3-hydroxyphenylalanine, following hydroiodic acid hydrolysis, as a marker for PM (Wakamatsu et al., 2002). Values for EM and PM were derived by multiplying by factors of 80 and 26, respectively (Ito et al., 2011).

Statistical analyses

All data were assessed for normality using Shapiro-Wilk test and visual assessment of Q-Q plots. Questionnaire data on hair treatment was used to exclude hair samples from pigmentation analyses if they had undergone color-altering treatments, and to exclude hair samples from analyses of curvature and cross-sectional geometry if they had undergone texture-altering treatments (Supporting Information Document 3). Curvature irregularity and PM were non-normally distributed and were therefore log transformed (log10) prior to analysis. Two African individuals were completely removed from pigmentation comparisons due to missing data. One-way analysis of variance was applied to assess variation among groups for the following variables: average curvature, curvature irregularity, cross-sectional area and cross-sectional shape, TM, EM, and PM content. Mixed individuals are included in plots for visualization purposes, but not statistical analyses between regional groups as the sample of mixed individuals was too small and heterogeneous for these purposes. Levene's statistic was used to test for homogeneity of variance, after which either Hochberg or Games-Howell post hoc tests were considered for comparisons among groups. Regression analyses were used to test for the effect of cross-sectional shape on average curvature. Additionally, correlation analysis was used to test the relationship between TM (spectrophotometric) and EM + PM (HPLC). Inter-rater reliability of the digitized measure of curvature was tested on the mean

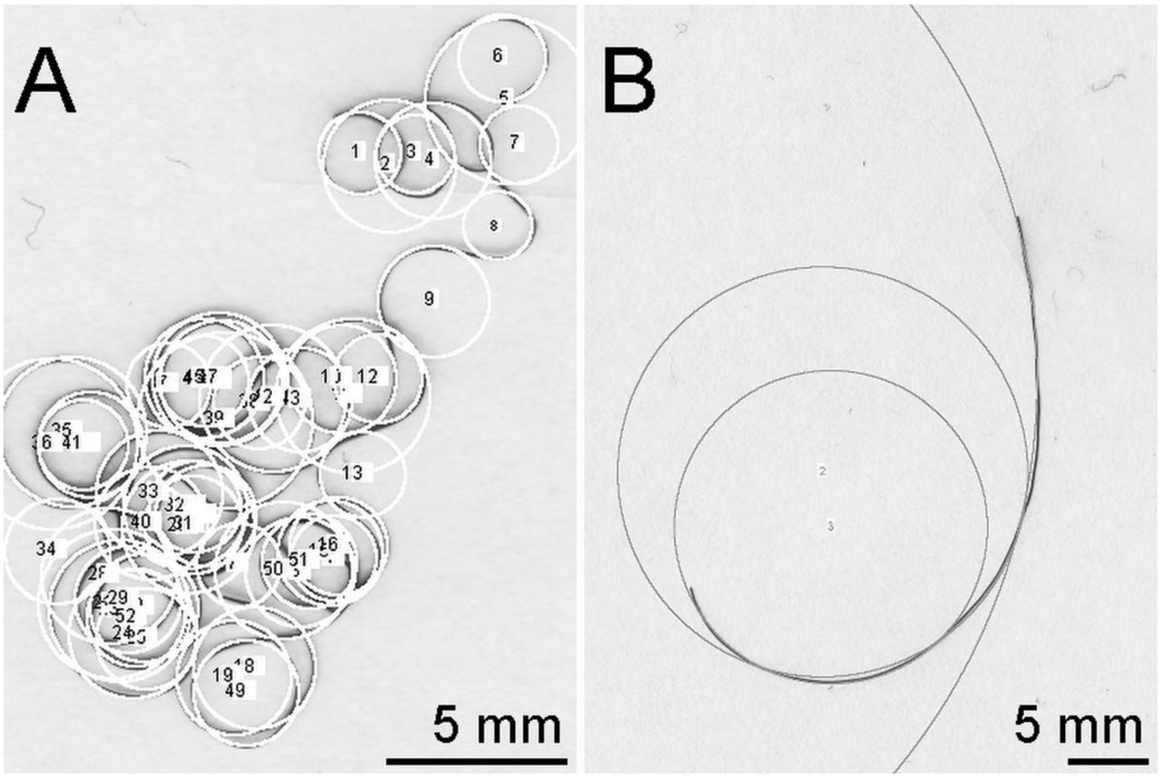

Fig. 1. Comparison of curvature measurements from a highly curled sample (**A**) and a relatively straight hair sample (**B**).

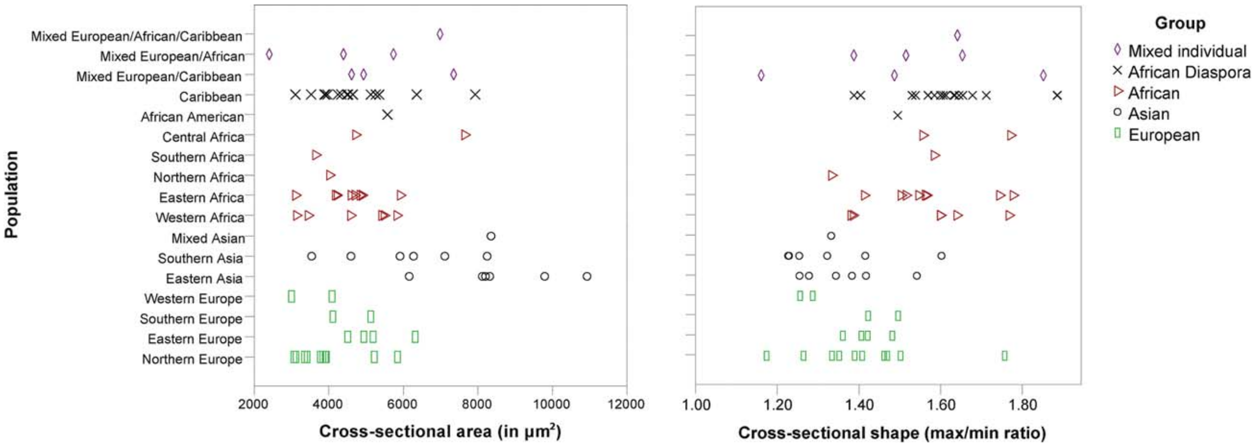

Fig. 2. Data plots of variation in cross-sectional area and cross-sectional shape by population.

radius of curvature of a subset of hair fibers using the intraclass correlation coefficient based on absolute agreement of single measures (Bartko, 1966; Shrout and Fleiss, 1979; Hallgren, 2012). All statistical analyses were undertaken using SPSS Statistics 20.0 (IBM, Armonk, NY), output of which is available (Supporting Information Document 4).

RESULTS

Cross-sectional geometry

Figure 2 displays values of cross-sectional area and cross-sectional shape across populations. Mean values for cross-sectional area were significantly different among groups ($F = 16.230$, $dF = 3$, $P < 0.001$). Values were significantly higher in the Asian group, while differences among the other groups were nonsignificant. While East Asians show values much larger than other populations, there appears to be a large amount of overlap between South Asians and other populations. Mixed individuals plot largely with other non-East Asian populations. Cross-sectional shape was also significantly different among groups ($F = 15.425$, $dF = 3$, $P < 0.001$). African and African Diaspora groups had significantly more elliptical cross-sections than the European and Asian groups, but were not significantly different from each other. Variability in cross-sectional shape was relatively similar across populations with significant overlap (Tables 2 and 3, Fig. 2).

TABLE 2. Mean values (and SD) for comparisons of curvature, cross-sectional geometry, and pigmentation variables which were significantly differentiated among groups.

			African	European	Asian	African Diaspora
		N	18	18	13	18
Curvature	Average curvature		0.395 (0.20)	0.042 (0.02)	0.032 (0.02)	0.484 (0.12)
Cross-sectional geometry	Area (in μm)		4690 (1119)	4266 (980)	7352 (2034)	4746 (1113)
	Shape (max/min)		1.569 (0.14)	1.402 (0.13)	1.354 (0.12)	1.614 (0.13)
		N	18	17	12	13
Pigmentation	TM (μg/mg)		23.21 (3.7)	8.07 (3.5)	20.28 (4.2)	23.75 (4.5)
	Eumelanin (μg/mg)		22.90 (4.2)	9.05 (3.9)	21.44 (3.9)	21.72 (4.1)

TABLE 3. P*-values (2-tailed) for comparisons of curvature, cross-sectional geometry, and pigmentation variables, which were significantly differentiated among groups.*

			African	European	Asian	African Diaspora
		N	18	18	13	18
Curvature	Average curvature	African		**<0.001**	**<0.001**	0.399
		European	**<0.001**		0.511	**<0.001**
		Asian	**<0.001**	0.511		**<0.001**
		African Diaspora	0.399	**<0.001**	**<0.001**	
Cross-sectional geometry	Area	African		0.626	0.003	0.999
		European	0.626		**0.001**	0.525
		Asian	**0.003**	**0.001**		**0.003**
		African Diaspora	0.999	0.525	**0.003**	
	Shape	African		**0.002**	**<0.001**	0.873
		European	**0.002**		0.880	**<0.001**
		Asian	**0.001**	0.880		**<0.001**
		African Diaspora	0.873	**<0.001**	**<0.001**	
Pigmentation		N	18	17	12	13
	TM	African		**<0.001**	0.259	0.999
		European	**<0.001**		**<0.001**	**<0.001**
		Asian	0.259	**<0.001**		0.170
		African Diaspora	0.999	**<0.001**	0.170	
	Eumelanin	African		**<0.001**	0.907	0.959
		European	**<0.001**		**<0.001**	**<0.001**
		Asian	0.907	**<0.001**		>0.999
		African Diaspora	0.959	**<0.001**	>0.999	

Curvature

Figure 3 displays the values of average curvature and irregularity across populations. Average curvature was significantly different among groups ($F = 60.970$, $dF = 3$, $P < 0.001$). Mean values for average curvature of African and African Diaspora groups were not significantly from each other (Tables 2 and 3), but both had significantly higher average curvature than Asian and European groups. Asian and European groups were not significantly different from each other in average curvature. European and Asian populations display low average curvature, indicating relatively straight hair, with East Asians clustering together around the lowest values. African populations show the widest range of variation, with West Africans showing generally higher values and East Africans spanning from relatively low to high values. African Diaspora values largely overlapped with West African data points and Mixed individuals were mainly intermediate between European/Asian groups and West Africans and the African Diaspora (Fig. 3). No significant differences among groups were found for irregularity ($F = 2.339$, $dF = 3$, $P = 0.082$). Interobserver reliability of the curvature measurement method was calculated to have an intra-class correlation coefficient of 0.978 with 95% CI (0.943, 0.992) based on absolute agreement of single measures (Supporting Information Document 5).

Effect of cross-sectional shape on hair fiber curvature

Figure 4 shows a plot of cross-sectional shape values against average curvature. In a linear regression including all samples, the cross-sectional shape was a significant predictor of average curvature ($P < 0.001$, $R^2 = 0.294$). As the African and African Diaspora groups both had higher curvatures and more elliptical cross-sections, we ran the tests again to test for a linear relationship between these variables within groups and found that cross-sectional shape was not a significant predictor of average curvature within groups.

Hair pigmentation

Figure 5 shows the values of TM (by spectrophotometric method) and EM (by HPLC method). Mean values

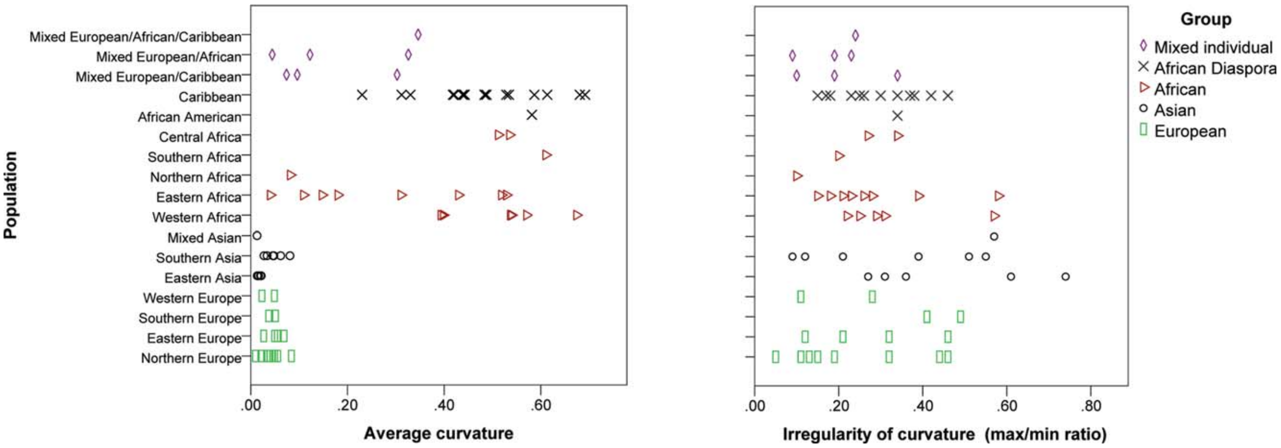

Fig. 3. Data plots of variation in average curvature and irregularity of curvature by population.

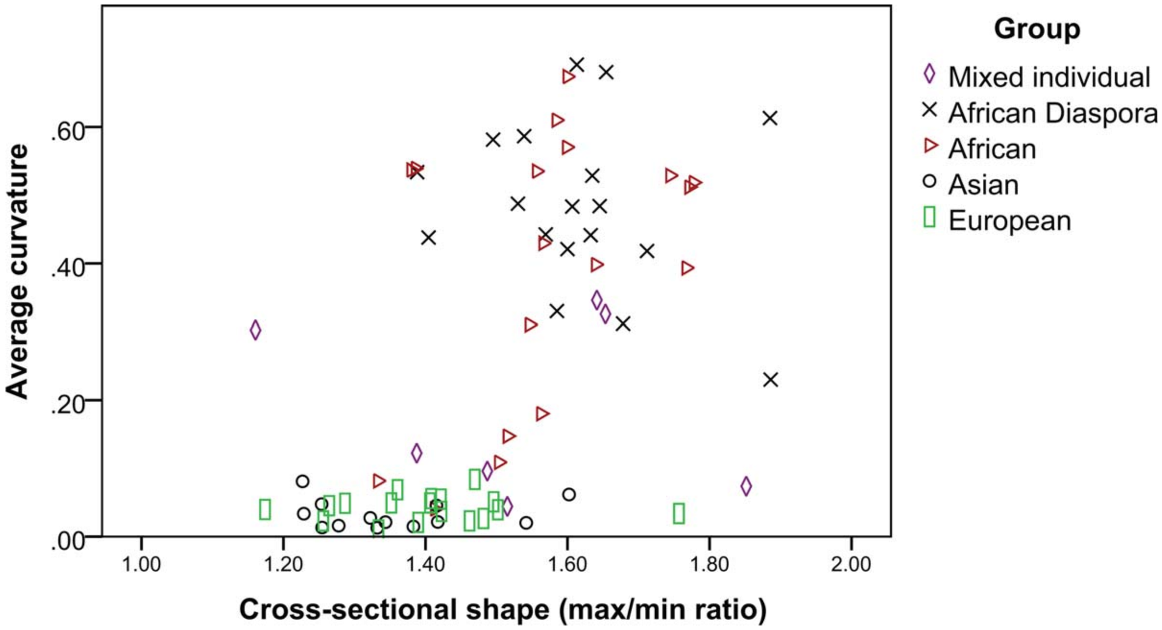

Fig. 4. Scatterplot of cross-sectional shape against average curvature.

were significantly different among populations for both TM ($F = 57.091$, $dF = 3$, $P < 0.001$) and EM ($F = 43.264$, $dF = 3$, $P < 0.001$). The European group had significantly lighter hair than other groups according to TM and EM analyses (both $P < 0.001$). Variation within groups for both TM and EM was similar (Tables 2 and 3, Fig. 5). No significant differences among populations were found for PM (by HPLC method) ($F = 0.898$, $dF = 3$, $P = 0.448$), although the only red-haired participant in our sample can be seen as an outlier in Figure 6. Figure 7 displays the correlation between TM and EM + PM for the total sample ($R = 0.956$, $P < 0.001$). We found differences in this correlation among groups with African populations showing significant but lower correlations than other groups (Table 4). Considering the possibility of age as a factor (as African and African Diaspora populations had a wider age range), we ran the correlation analyses again restricting the age sets to 17-25 and found that the correlation for African and African Diaspora groups improved slightly, but that the significance of this correlation declined. Correlation between TM and EM remained slightly lower for the African group (Table 3).

DISCUSSION

The aim of this study was to evaluate a number of quantitative methods for the assessment of scalp hair fiber curvature, cross-sectional geometry, and pigmentation based on their application to a limited sample of individuals from diverse populations. While the sample composition was such that it did not allow for analysis of variation based on age and sex, among other potentially informative variables, we were able to carry out exploratory data analysis based on our measurements of hair variables that revealed certain patterns among populations that warrant further research to evaluate any adaptive value or demographic effects in the evolution of human hair diversity.

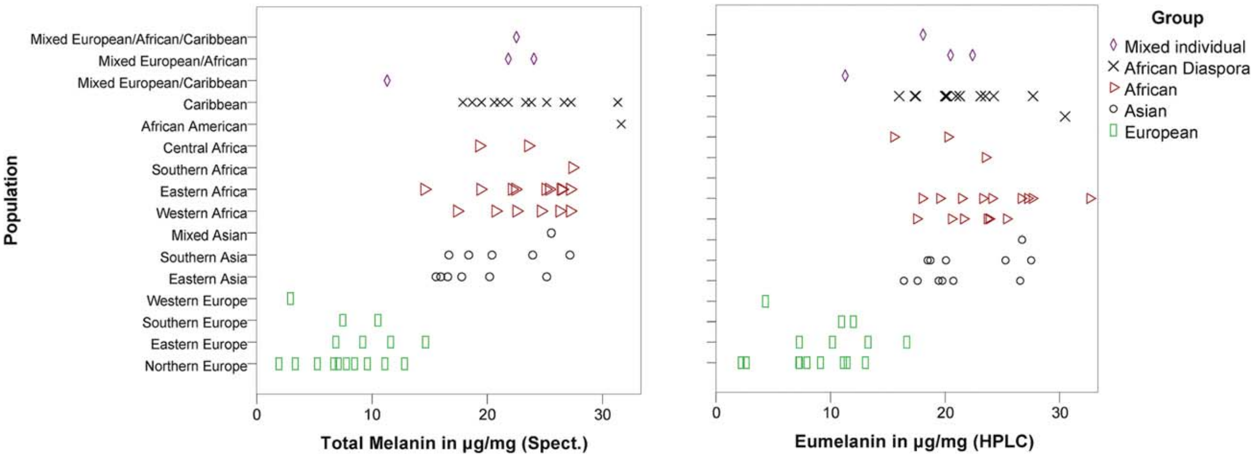

Fig. 5. Data plots of variation in spectrophotometric measurement of TM and HPLC measurement of EM by population.

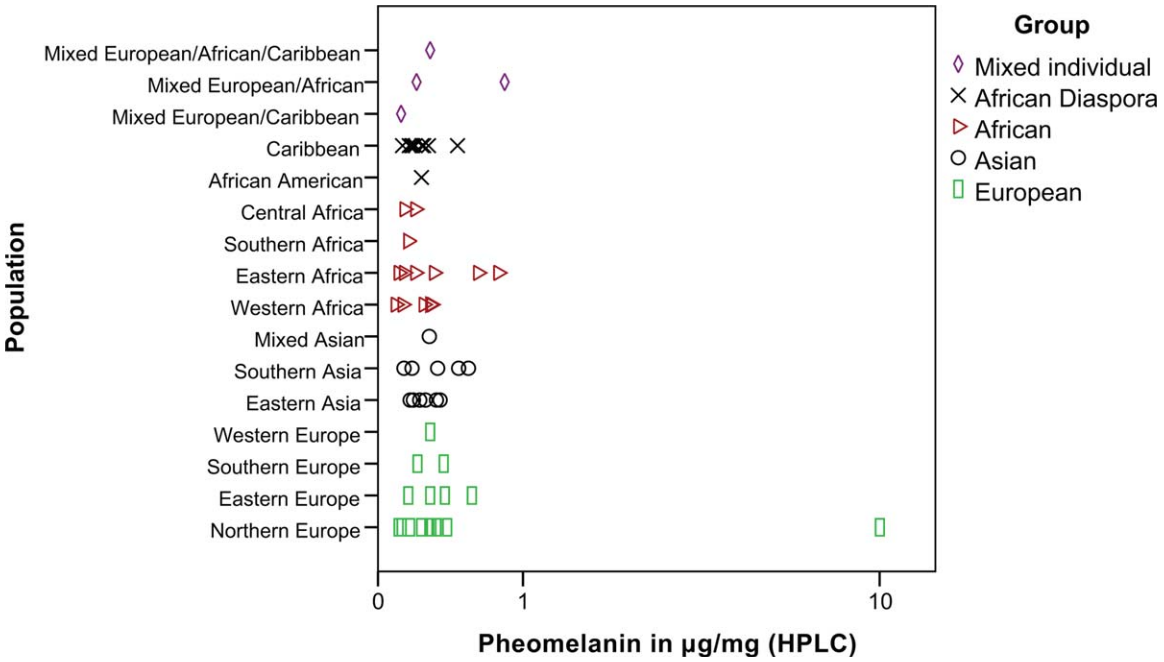

Fig. 6. Data plots of variation in HPLC measurement of PM by population. Outlier represents the single red-haired participant in the study.

Cross-sectional geometry

The method of assessing cross-sectional geometry presented herein involves embedding fibers in resin for a transverse view, as in certain other studies (e.g., Fujimoto et al., 2008a,b). While it is possible, and arguably simpler, to assess cross-sectional diameter by collecting multiple measurements along the fiber longitudinally (e.g., Hrdy, 1973), the relative advantage of a transverse view of the fiber is that it allows for the assessment of area, as well as minimum and maximum diameter at one particular point on the fiber. Furthermore, the longitudinal measurement of hair fiber diameter may be confounded by twists along the hair fiber, which may give the impression of a highly variable hair diameter in twisted hair fibers with an elliptical cross-sectional shape. However, since the transverse approach only characterizes one single data point, cross-sections for multiple hair fibers should be analyzed to gain a more representative of the individual. Ideally, future studies should attempt to collect transverse measurements from, not only multiple hairs in an individual, but also, multiple points along a single hair fiber in order to gain an improved understanding of the variability of cross-sectional geometry throughout the growth of hair.

Nevertheless, the results of this study confirm patterns of variation among populations that have been reported previously. Hair fibers in our Asian group were significantly thick and, among this group, hair fibers had particularly large cross-sectional areas in our East Asian population, which was composed of individuals of Chinese and Korean descent (see Supporting Information Table 1 for breakdown of samples by country of ancestry). The particular thickness of hair in East Asian

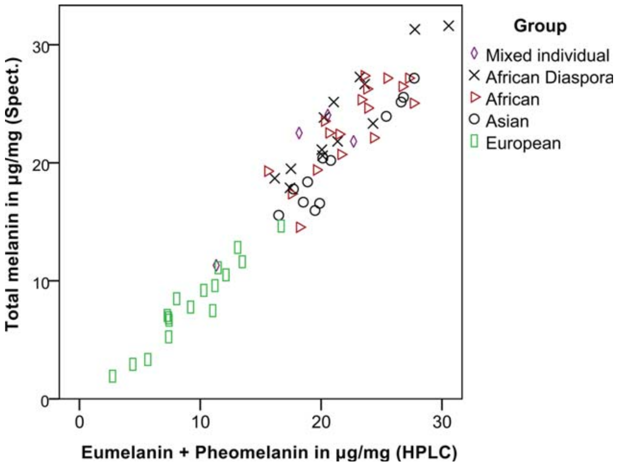

Fig. 7. Scatterplot of HPLC measurement of EM + PM against spectrophotometric measurement of TM content.

TABLE 4. Exact p-*values (2-tailed) for correlations between spectrophotometric assessment of TM and HPLC assessment of EM + PM within groups.*

	N	*R*	Exact *P*
African	18	0.771	0.00018
European	17	0.962	7.53×10^{-10}
Asian	12	0.958	9.40×10^{-7}
African Diaspora	13	0.930	4.19×10^{-6}
Age Restricted (17–25)	*N*	*R*	Exact *P*
African	11	0.867	0.00054
European	17	0.962	7.53×10^{-10}
Asian	12	0.958	9.40×10^{-7}
African Diaspora	5	0.966	0.00748

populations has been noted in the past (Vernall, 1961; Hrdy, 1973) and in recent years this trait has been linked to a mutation in the EDAR locus which occurs at a high frequency in these populations (Fujimoto et al., 2008a,b; Mou et al., 2008). The particularly large variability of cross-sectional area in our results for the Asian group can largely be explained by our grouping South and East Asians together. Our South Asian population included individuals of Indian, Sri Lankan, and Pakistani origin, who overlapped considerably with both East Asians and other populations in terms of hair thickness. The presence of the underlying EDAR mutation has been noted in some Thai and Indonesian populations (Fujimoto et al., 2008a) as well as, to a lesser extent, some Indian populations thought to have a certain amount of admixture with East Asian populations (Chaubey et al., 2011).

The evolutionary causes of these strong signs of positive selection for the EDAR mutation in East Asians remain obscure as it appears to have pleiotropic effects associated with dental morphology and changes to the mammary and eccrine sweat glands (Mou et al., 2008; Kamberov et al., 2013). If the selective pressure was indeed for thicker hair, the adaptive value could be related to the presence of a medulla (a hollow layer inside the hair shaft), as, in non-human mammals, medullae are thought to serve an insulating function (Deedrick and Koch, 2004). While medullae are frequently absent in human hair, or appear discontinuously along the length of the shaft, their presence is highly correlated with the thickness of the hair fiber (Banerjee, 1962; Das-Chaudhuri and Chopra, 1984). However, more data must be collected on the distribution of this particular allele and the distribution of thick hair among populations in relation to prehistoric climatic data in order for any thermoregulatory hypothesis to be tested. While the sample composition of this study did not allow for the testing of sexual dimorphism or effect of age in cross-sectional area, this has been reported elsewhere and may account for a proportion of the variability in our data (Wynkoop, 1929; Trotter, 1930; Das-Chaudhuri and Chopra, 1984).

With regards to cross-sectional shape, populations in our dataset largely overlapped, with only African and African Diaspora populations being significantly distinguished as more elliptical in shape. While some in the literature characterize Asian hair as being distinctly round, African hair being distinctly elliptical and European hair being intermediate (e.g., Vernall, 1961), others note the significant overlap between populations (Trotter, 1930). Our data, although based on a small sample size, shows a substantial degree of overlap with the mean values of African and African Diaspora being slightly higher, signifying more elliptical cross-sections. The significance of variation in cross-sectional shape in relation to curvature is discussed in further detail below.

Curvature

Hair fiber curvature is a difficult trait to quantify. Curvature itself, from a mathematical perspective, is complex and can be described in a number of ways, the most common of which is as the reciprocal of the radius of a circle fitting its curve – ergo, curvature is represented as a deviation from a straight line (Lee, 1997). Complicating matters even further is the nature of the hair fiber, curving in three-dimensional space, with a diameter of around 40–120 µm and lengths on an order of magnitude in the tens of centimeters. These factors likely contribute to the reason why hair curvature has largely been described qualitatively (Trotter, 1938; Hooton, 1946; Garn, 1948; Medland et al., 2009) even though it is a continuous trait (Hrdy, 1973; De La Mettrie et al., 2007; Loussouarn et al., 2007). Hrdy (1973) proposed curvature of hair could be quantified by placing the hair between two glass slides, thus reducing the curvature to two dimensions, and determining the radius of curvature by matching each curve with the arc of a fitting circle and calculating the average curvature. Quantification of hair fiber curvature has since been based on this method (Bailey and Schliebe, 1985; De La Mettrie et al., 2007; Loussouarn et al., 2007) with the main variation in the curvature method used by De La Mettrie et al. being that they take into account only the smallest curvature in a hair fiber (this method is used also by Loussouarn et al., 2007).

The method presented in this article is a digital application of Hrdy's original method of quantifying curvature and can be used to calculate the average curvature of a hair fiber as well as the maximum to minimum curvature ratio (details in Supporting Information Document 2). The inter-rater reliability for this method is high, though we are not able to compare this with other studies of curvature quantification for the lack of comparable reliability estimates. The use of this digital method has a number of advantages. Primarily, the use of free software makes it accessible and the use of ImageJ, in particular, allows for the exact tracing of a curve, rather than estimating it with an overlay. In practice, this accommodates the measurement of relatively straight hairs that still show some curvature. However, the method must be improved further, as the average curvature variable does not take into account that the various curvatures measured do not contribute equally to explaining the average curvature of the entire hair fiber (i.e., some measurements should be weighted more heavily than others). Neither does the method distinguish between the continuous curvature and other features that have been described as “crimp” and “kinking” or “twisting” (Hrdy, 1973; De La Mettrie et al., 2007). Preferably, if the two-dimensional measurement of hair fiber curvature in a single metric is to be pursued, an algorithm should be developed to calculate curvature along a traced hair fiber to eliminate any potential for interobserver error. Moreover, as curvature is defined by the reciprocal of the radius, any variability among highly curled hairs will be augmented, while straight and wavy hairs are packed together on the other end of the spectrum and cannot be distinguished well, as these hairs do not deviate far from a straight line using this mathematical definition (see Fig. 3).

Nonetheless, our results echoed previous studies, distinguishing African and African Diaspora populations as having highly curled hair (Hrdy, 1973; Bernard, 2003; Thibaut et al., 2005, 2007; Loussouarn et al., 2007). This study did not find significant differences between the curvature of European and Asian groups, though it has been suggested that Asian hair is typically straight, while European hair exhibits a great range of variation (Medland et al., 2009; Piérard-Franchimont et al., 2011). This could be in part due to insufficient statistical power on our part to detect these differences, but it is likely related to our inclusion of South Asians in the Asian group (as Fig. 3 indeed confirms East Asians have straighter hair). Most literature referring to differences between European and Asian populations discuss more specifically the differences between Northern/Western European populations and East Asians stemming from a tri-partite view of global diversity (i.e. European, Asian and African), which does not overlap perfectly with continental designations (Lindelöf et al., 1988; Franbourg et al., 2003; Piérard-Franchimont et al., 2011).

In our sample, an interesting pattern was the difference between East African and West African individuals (see Fig. 3). This result supports the observation of curvature variability within African populations as noted in previous studies (De La Mettrie et al., 2007; Loussouarn et al., 2007) and cautions against the *a priori* categorization of “African hair” as a homogenous category (Hrdy, 1973; Ogle and Fox, 1998). In this study, East Africans spanned a large range of the curvature spectrum, overlapping with South Asians and European populations, as well as West Africans. Individuals of the African Diaspora overlapped largely with West Africans, while individuals of mixed European and African/Caribbean ancestry fell intermediate between their two ancestral groups. The work of De La Mettrie and Loussouarn’s group highlights the rich diversity of hair form around the world that cannot adequately be described by classifications of “African,” “Asian,” and “European” hair types (De La Mettrie et al., 2007; Loussouarn et al., 2007). While we wholeheartedly agree with their statements, we would however equally emphasize that this variation is not distributed randomly across the globe and understanding its exact distribution and the evolutionary processes that have shaped it would be of anthropological interest. Improving an objective approach to the quantification of hair form, which takes into account its continuous nature, rather than attempting to artificially categorize it, is necessary for the testing of evolutionary hypotheses and comparisons of this trait against genetic distance between populations.

Attempts to quantify curvature must be informed by a comprehensive understanding of the various factors contributing to the shape of the hair fiber. In this sense, it may be necessary to describe hair form beyond the two-dimensional curvature of the hair fiber (e.g., Hrdy, 1973), perhaps even using a compound metric encompassing various features of the hair fiber (as per De La Mettrie et al., 2007; Loussouarn et al., 2007). However, for this purpose, it is imperative to accurately distinguish independent contributors to hair form from mechanistic consequences of various features on the shape of the hair fiber. For example, if the “kinking” and “crimp” described by (Hrdy, 1973) or “number of waves” and “twists” described by De La Mettrie et al. (2007) are increasingly found in highly curled hairs, they may be functional correlations rather than independent contributors to hair form. Variation in hair fiber shape has been ascribed to various factors, including nutrition, proportion and distribution of orthocortical and paracortical cells, speed of growth, chemical composition, as well as shape and size of the hair follicle (Campbell et al., 1975; Kulkarni, 1983; Lindelöf et al., 1988; Jafari et al., 2005; Thibaut et al., 2005; Kajiura et al., 2006; Bryson et al., 2009; Robbins, 2012).

Classical anthropologists had noted early on the “flat” or elliptical cross-sections in African hair and the round form of (East) Asian cross-sections and had linked this to the differences in respective curliness or straightness of these individuals’ hair, leading to the theory that cross-sectional shape dictates curliness (Pruner-Bey, 1877). This theory on the cause of hair curvature has since been denied on the basis that there is not a strict association between cross-sectional shape and degree of curvature (Garn, 1948; Hrdy, 1973). Our results confirm that there is indeed a correlation between cross-sectional shape and average curvature, but that this correlation was not significant within groups (i.e., once differences in cross-sectional shape were taken into account). Based on the literature and our results, it seems likely that there are different factors contributing to hair curvature, and these factors may contribute differentially to various populations. For instance, the mutation in EDAR associated with thicker hair is also associated with straighter hair (Tan et al., 2013). And while our study found no significant patterns in curvature irregularity between populations, Hrdy (1973) noted that high irregularity distinguished Melanesians from African populations with regards to curvature. Furthermore, while beyond the scope of our study, it has been noted that individuals’ hair form changes over a lifetime (Trotter, 1930) which may be related to factors still different from those contributing most to differences between populations. Trotter in particular notes how hair in European individuals is lighter, straighter and has a smaller cross-sectional diameter at younger ages and older ages (Trotter, 1930). It may be worth considering the inter-relationship between these factors on the level of the individual, as melanin granule deposition may potentially contribute to the size and shape of terminal hair shaft.

As for the evolutionary significance of this variation in hair form, it has been suggested that tightly curled hair, as found in many individuals of African descent, confers some adaptive benefit with regards to thermoregulation, namely, cooling the scalp more efficiently (Jablonski, 2006). In this light, the diversity in hair form found in Africa previously (e.g., Loussouarn et al., 2007) and in our study poses some stirring questions. If curled hair is a thermoregulatory adaptation, why does it present more extremely in West Africans? If both East and West African ranges of hair curvature convey thermoregulatory benefits, is there perhaps a threshold after which further curvature does not provide additional adaptive benefits? If so, is all variation after that threshold neutral or sexually selected? The possibility of a "threshold" situation where a trait is both variable and selectively constrained has been suggested as an explanation for pigmentation variation in African and Melanesian populations (Relethford, 2000; Norton et al., 2006). It is, however, possible that non-African admixture in certain East African populations is the cause for the variability in hair curvature (Hodgson et al., 2014). The similar range of curvature in individuals of mixed European and African descent to East Africans in our sample is thus an interesting comparison. If non-African admixture is indeed responsible for East African ranges of curvature, it would have interesting implications for our understanding of the intensity of selective pressures on dark skin as opposed to tightly curled hair. Dark skin is strongly correlated to latitude, independently of genetic distance, but tightly curled hair is distributed much more sporadically around the world.

Pigmentation

Non-European hair is frequently described as 'uniformly' dark (Trotter, 1930; Frost, 2006), however the results of our study strongly suggest that when objectively measuring melanin content of hairs, there is a comparable amount of variation among populations (Fig. 4). Though hair color is often described categorically, there have been many attempts to quantify this continuous trait, including recently the increasing use of reflectance spectrometers and tristimulus colorimetry methods (e.g., Norton et al., 2014, 2015a). The advantages of such methods over the chemical method used in this study is lower relative cost and time. However, these methods still may not be able to distinguish the fine-scale variation existing in the darker end of the spectrum, which is of particular importance to understanding non-European variation (as concluded by Norton et al., 2015a). Categorical descriptions of hair color, spectrometers, and colorimetry echo the notion of a greater perceived variability in European hair color, which may be important in hypothesizing the effect of sexual selection in these populations. Yet, the variability revealed by the chemical estimation of melanin content stresses the importance of considering the ways in which natural selection may be acting on variation we do not readily perceive.

The two methods for pigmentation analysis used in this paper are the spectrophotometric estimation of TM and the use of HPLC to estimate EM and PM based on their degradation products. In the current sample, results confirmed a lower range of EM and TM in European populations and trace amounts of PM in all but one European individual, although it may be possible that PM variation plays a larger role in populations yet to be analyzed. Both spectrophotometric (TM) and HPLC (EM + PM) methods were previously found to be highly correlated (Ito et al., 2011). Interestingly, in our study, there was a slightly lower (although still highly significant) correlation between these two estimates of melanin content for African and African Diaspora populations (Table 4). A possible interpretation of the lower correlation between TM and EM + PM in these populations is a higher variation in dopachrome tautomerase (DCT) activity, which plays a key role in the biosynthesis of one particular type of EM–dihydroxyindole-2-carboxylic acid (DHICA), the type of EM quantified by our current HPLC method. Another EM, 5,6-dihydroxindole (DHI), also contributes to the EM of hair (which would be included in the TM content estimate), and may do so even to a larger extent than DHICA-EM (Commo et al., 2012). As DCT activity dictates DHICA-EM, it is possible that a higher variability in DCT activity in African populations could lead to a weaker correlation between TM and EM, even when age is taken into account. This complexity underscores the necessity of taking into account various lines of evidence when discussing variation in hair pigmentation. While categorical descriptions, reflectance, and colorimetry methods may inform us on perceived hair color, we must also consider variation in melanin content, the ratio of different melanins, and the distribution and size of melanosomes before we can evaluate the effect of evolutionary processes such as neutral, natural, or sexual selection on the variation that exists in modern humans.

CONCLUSION

The hair samples analyzed here represent only a fraction of global variation in scalp hair fiber shape and pigmentation. Nevertheless, this study has demonstrated the usefulness and limitations of a number of methods for the quantification of hair fiber shape and pigmentation. Future research should include populations from regions that have been habitually understudied in the hair variation literature, amongst which are: Central and Western Asia, Eastern and Southern Europe, and Oceania, as well as indigenous populations of America. Furthermore, the use of quantitative methods in hair variation research will address the main limitation faced thus far in effectively genotyping hair variants: the lack of standardized phenotype assessments able to distinguish the continuous and fine-scale variation present among and within populations (Rees, 2003; Norton et al., 2015a). Using these quantitative methods and improving them where limitations are described, future studies will be better equipped to evaluate the effects of selection, as well as neutral variation, not only in humans, but also in non-human apes. Such an endeavor would greatly contribute to our understanding of the evolutionary factors that drove *Homo sapiens* to become the Nearly Naked Ape.

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