Morphological Uniqueness: The Concept and Its Relationship to Indicators of Biological Quality of Human Faces from Equatorial Africa

Karel Kleisner

Department of Philosophy and History of Science, Faculty of Science, Charles University, 128 00 Prague, Czech Republic; karel.kleisner@natur.cuni.cz

Abstract: Facial symmetry, averageness, and the level of sex-typical development of dimorphic traits are traditionally associated with various biological quality indicators and should be, therefore, preferred in mate choice. The aim of this study is to propose a concept of morphological uniqueness and uncover its possible associations to putative phenotypic cues of biological quality. I employed a combination of geometric morphometric and Bayesian multiple regression to analyze 300 Cameroonian faces, while an additional 1153 faces from eight distinct populations from across four continents were used as a reference sample of the global population to calculate the morphological uniqueness of Cameroonians. I found that morphological uniqueness is positively associated with a feminine facial shape in women and negatively with morphological masculinity in men. Facial symmetry was positively associated with female faces with greater levels of uniqueness; the result for male faces was inconclusive. The faces of both sexes perceived as more attractive had lower levels of morphological uniqueness. Facial distinctiveness showed no relationship to morphological uniqueness in either sex, which indicates that morphological uniqueness and distinctiveness are two complementary approaches to studying facial typicality. In the conclusion, the evolutionary significance of the proposed concept and its potential applicability is discussed.

Keywords: morphology; geometric morphometrics; adaptation; facial asymmetry; sexual dimorphism; distinctiveness; typicality; human face; geographic variation

1. Introduction

A face reflects both the individual’s genetic legacy and the imprint of environmental influences. Ancestors of modern humans inhabited various environments and were therefore exposed to different natural and social conditions [1,2]. Like all living organisms, humans acquired along their evolutionary path various genetic, physiological, morphological, and behavioral adaptations [3–5]. To understand the local adaptations and their evolutionary circumstances, one should thus look at the group-specific characteristics associated with particular environmental and social conditions.

The genomics of local human adaptations has recently undergone a rapid development [4]. The same does not hold of the complementary study of local morphological adaptations. This asymmetry might be due to an unjustified but often held belief that the morphological dimension of living organisms is evolutionarily less important than the genetic one [6]. This situation is further aggravated by insufficient conceptualization of morphological phenomena and a slower development of the technical means for their study, though one can see a potential to change [7].

Morphologically unique facial traits typical of particular human populations may have been shaped by (1) ecological selection, that is, environmental adaptations to local climate, (2) sexual selection, meaning having a role in the mating context, or (3) inheritance...
from people who lived (and/or migrated to) the same place in the past, or (4) it may be a byproduct of organizational mechanisms underlying some other advantageous processes in human physiology. Still, regardless of whether such morphologically unique characteristics are proper adaptive structures or neutral traits, they should not be detrimental to their bearers with respect to their reproduction, that is, they should not systematically decrease their biological fitness.

It has traditionally been assumed that climate is a possible ecological cause of variations of facial morphology [8–10]. Anthropologists suggested, for instance, that people who inhabit wetter and stable climates tend to have wider faces and a broader nasal architecture [11–13]. Whether this particular morphology is an adaptation that helps prevent overheating in demanding climatic conditions is, however, yet to be ascertained [14,15]. Moreover, the mode of subsistence and associated food-producing behavior also seem to significantly affect the morphological variation of human faces. For instance, nomadic pastoralists from the Sahel belt tend to have narrower faces with thinner lips and longer and narrower noses, while sedentary farmers from the same area have wider and rounder faces with fuller lips and shorter, robust noses [16]. There is also evidence from nonhuman animals to the effect that morphologically unique features on an intraspecific level correspond to particular environmental conditions and ways of life. For instance, it has been shown that certain unique traits of brown bears (Ursus arctos) from Etorofu Island, such as their greater size and the presence of white pelage fur, correlate with their feeding habits, in particular, with preying on salmon [17].

When it comes to sexual selection, it has been demonstrated that preference for particular facial traits plays a central role in the mate choice of both humans and nonhuman animals. The evolutionary significance of these features of appearance is based on the fact that they can communicate their bearers’ biological quality, including health, developmental stability, genetic quality, and reproduction potential, including parental investment. In other words, high-quality individuals should be preferred as partners for reproduction, due to their capacity to provide direct benefits (protection, energy resources, and investment in offspring) but also indirect benefits, such as inherited qualities (so-called ‘good genes’) that may lead to increased pathogen resistance, better coping with a handicap, optimized compatibility of sexual partners, etc. [18–22]. Specifically in humans, numerous traits are considered attractive when they are more symmetrical, sexually typical, and closer to the population average [23]. This holds especially for shape features but may not be true or applicable to some non-shape traits, such as skin and eye color, which are often preferred in their unusual and rare variants, probably due to frequency-dependent sexual selection [24–26]. Of course, there are many other cues to facial attractiveness: in addition to shape and color traits, skin smoothness and specific makeup and hairstyling also influence facial preferences [27–33]. These are, however, outside the scope of the current, purely morphological analysis.

In case of facial morphology, the level of symmetry, sexual dimorphism (facial masculinity and femininity), and averageness (vs. distinctiveness) are traditionally viewed as important cues of facial attractiveness. In short, one can expect that more symmetrical, average, and masculine (in case of men)/feminine (in case of women) faces will be perceived as more attractive. Recent research, however, shows that this holds only in part. Interactions with the sex of the trait bearer, trait perceiver, hormonal status, health status, environment, and other variables must also be taken into account [34–38]. This study, though, does not aim at disentangling the complex dynamics of the abovementioned fitness indicators and their relation to biological quality.

The aim of this paper is twofold. First, to introduce the concept of morphological uniqueness, which allows for quantification of traits which are unique to—though not necessarily most common in—a target population. This metric emphasizes those features which characterize a particular population against the background of all other members of the same species (or any other group). The second aim of this paper is to explore whether morphological uniqueness reflects possible adaptive benefits associated with pu-
tative fitness indicators, such as locally perceived facial attractiveness, sexual dimorphism, symmetry, and averageness (i.e., intrapopulational typicality).

By morphological uniqueness, I mean the relative occurrence (to other populations) of structurally unique features rather than some absolute presence/absence of a specific trait. Morphological uniqueness refers to continuous changes in shape variation rather than to the clear-cut presence or absence of a trait. I hypothesize that morphologically unique traits could reflect adaptations to local socioenvironmental conditions, which is why I predict (1) that they should be positively associated with intrapopulation measures of biological quality, and (2) that faces with pronounced unique traits should be locally preferred.

2. Materials and Methods

Facial configurations. In total, shape coordinates based on 1453 facial images were used for calculations in this study. The target population is represented by 300 faces (150 men, 150 women) of Cameroonian origin. Facial configurations other than Cameroonian were used solely as a global reference population to calculate morphological uniqueness. The database of shape coordinates consisting of Cameroonian, Czech, Colombian, Brazilian, Romanian, Turkish, British, and Namibian faces was published in a previous study [39]. This freely accessible dataset of facial shape coordinates was further augmented by a sample of 136 Vietnamese facial configurations (86 men, 50 women) to increase the representativeness of global population of facial morphologies. Sample sizes of all facial photograph subsets are accessible in the Supplementary Material (Table S1).

Attractiveness judgment. Cameroonian raters assessed the stimuli on a verbally anchored seven-point Likert scale, spanned from 1 (not at all attractive) to 7 (very attractive/masculine/feminine face). Each rater rated 50 facial portraits of the opposite sex on a 14-inch laptop screen. Each rater judged the photographs in randomized order. No time constraint was set on the rating procedure. Raters were mostly local students of the University of Buea in an Anglophone region of South-West Cameroon. See Table S2 for sample sizes and descriptive characteristic Cameroonian male and female raters.

Procrustes Analysis. Facial morphology was characterized by 72 landmarks, including 36 semi-landmarks that denote curved features and outlines (see Figure S1 for landmark positions and definitions). Shape coordinates (N = 209,232) of all 1453 facial configurations were entered into a general Procrustes analysis (GPA) using the `gpagen()` function in the Geomorph package in R [40,41]. Procrustes-aligned configurations were projected into a tangent space. Semi-landmark positions were optimized based on minimizing the bending energy between corresponding points. Procrustes residuals were then symmetrized so that the left and right sides were reflected, and the original and mirrored configurations averaged. This was done by the `symmetrize()` function in the Morpho package [42]. Symmetrization was performed after semi-landmarks were slid along their tangent directions. Non-symmetrized shape coordinates were also retained and used to calculate the level of facial asymmetry.

Measurement error assessment. Measurement error was quantified as repeatability on a subsample of 99 faces. Each face was digitized twice. Using the `procD.lm()` function, I employed a Procrustes analysis of variance between individual faces and two digitized configurations of the same face (replicates). Repeatability was calculated as a ratio of two variances components. The component of among-individual variance was divided by the sum of among-individual and measurement error variance components [43]. Repeatability of digitizing precision between the two replicates was 0.99, which corresponds to a 1% measurement error.

Morphological Uniqueness (MU). Aligned symmetrized shape coordinates (Procrustes residuals) of the target sample (Cameroonian, N = 300) and the reference sample (all non-Cameroonian, N = 1153) of the global population were then used to calculate MU. The individual level of facial MU was calculated as follows: First, I defined an axis connecting the facial shape average of the target group (Cameroonian) and of the reference group. Secondly, each of the 1453 facial configurations was projected on this between-group axis
connecting the target and reference group means. Thirdly, I extracted only that part of the
two-group vector which represented projections of Cameroonian faces. The position
of each individual projection along this vector then corresponds to the relative expression
of an individual’s facial uniqueness. Finally, MU scores were reversed (multiplied by −1),
so that larger MU values indicate higher levels of morphological uniqueness. MU was
calculated separately for men and women’s faces.

**Sex typicality.** Procrustes residuals which resulted from a joint Procrustes fit of all Cameroonian female and male facial symmetrized configurations were used to compute
sex typicality: a morphological degree of individual development of sexually dimorphic
traits [39]. Then I expressed morphological differences between Cameroonian men and
women using a vector in facial morphospace, which connected the sex-specific averages.
Individual sex typicality scores were computed by projecting each face onto a vector linking
male and female averages. Women’s scores were inverted (multiplied by −1) to make sure
that higher values in both sexes express higher sex typicality, i.e., a more masculine shape
in men and a more feminine shape in women.

**Asymmetry.** The aligned coordinates after Procrustes fit were first laterally reflected
along the midline axis. The corresponding paired landmarks on the left and right sides of
faces were then relabeled and the numeric labels of landmarks on the left side swapped for
the landmark labels from the right side and vice versa. To measure asymmetry, Procrustes
distances between the original and the mirrored (reflected and relabeled) configurations
were calculated, whereby larger values indicate greater facial asymmetry. To estimate the
impact of measurement error on the assessment of facial symmetry, I calculated asymmetry
scores separately for each of the two replicates. When the asymmetry scores of first and
second replicate were compared, correlation between the scores of the first and second
replicate was tight (r = 0.984), which indicates a high level of precision.

**Distinctiveness.** Based on symmetrized Procrustes residuals of Cameroonian facial
configurations, distinctiveness was calculated as the Procrustes distance from the group
mean. The greater the distance, the more distinct (and less average) the face.

**Regression of facial shape to morphological uniqueness.** To address the shape variation
associated with morphological uniqueness in Cameroonian faces, symmetrized Procrustes
residuals were regressed on the vector of morphological uniqueness. This was done by the
`procD.lm()` function from the Geomorph R package, with the significance test based
on 9999 permutations. Shape changes related to MU were visualized by a thin-plate
spline interpolation function using the `plotReftoTarget()` function available in the Geomorph
package as a deviation from the average facial shape.

**Statistical analysis.** The `ulam()` function from the rethinking package was used to fit
Bayesian multiple regression [44]. Morphological uniqueness scores were set as a depen-
dent variable, while perceived attractiveness, sex typicality, asymmetry, distinctiveness,
BMI, and age of individuals were specified as predictors. Separate models were built for
men and women. The model was compiled into Stan syntax, which was used to sample
from the joint posterior probability distribution of likely parameter values [45]. A total of
10,000 samples from each posterior distribution were extracted using the Markov chain
Monte Carlo method. Unbiased, weakly regularizing priors were used for all model pa-
rameters (normal distribution with mean = 0 and SD = 0.2 for intercepts and mean = 0 and
SD = 0.5 for slopes). All variables were standardized prior to analysis. The analysis was
conducted using R, ver. 4.1.0.

**Ethics statement.** All parts of the experimental protocol conformed to current insti-
tutional, national, and international guidelines as well as the Helsinki Declaration. This
study does not include information or images that could lead to the identification of any
particular study participant. All procedures mentioned and followed were approved by
the Institutional Review Board of the Faculty of Science of the Charles University (protocol
ref. number 04/2020).
3. Results

Figure 1 shows density plots of the estimated parameter values for models fitted separately for men and women’s faces. Numeric results are summarized in Table 1. For a summary of bivariate correlations between all variables, see Figures S2 and S3 for women and men, respectively.

Figure 1. Density plots representing posterior distribution of estimated parameter values on a standardized scale for both sexes. MU = morphological uniqueness, int = model intercept, attr = facial attractiveness, sextyp = individual level of sexual shape dimorphism, asym = asymmetry, dist = distinctiveness, BMI = body mass index, age = age of the individual. Black error bars represent 95% compatibility intervals (CI) of the parameters, while circles denote the mean of each parameter estimate.

Table 1. A summary of posterior samples showing mean slope, standard deviation (SD), and lower (2.5% CI) and upper (97.5% CI) compatibility intervals (CI) for parameter values

| Sex   | Parameter                  | Mean Slope | SD   | 2.5% CI     | 97.5% CI     |
|-------|----------------------------|------------|------|-------------|--------------|
| Women | MU~Intercept               | 0          | 0.067| −0.132      | 0.131        |
|       | MU~Attractiveness          | −0.169     | 0.073| −0.313      | −0.025       |
|       | MU~Sex typicality          | 0.269      | 0.081| 0.11        | 0.427        |
|       | MU~Asymmetry               | −0.302     | 0.079| −0.457      | −0.147       |
|       | MU~Distinctiveness         | 0.006      | 0.073| −0.138      | 0.149        |
|       | MU~BMI                     | 0.185      | 0.077| 0.033       | 0.336        |
|       | MU~Age                     | −0.063     | 0.077| −0.215      | 0.089        |
|       | SD residuals (sigma)       | 0.875      | 0.052| 0.781       | 0.984        |
| Men   | MU~Intercept               | 0          | 0.07 | −0.138      | 0.138        |
|       | MU~Attractiveness          | −0.372     | 0.079| −0.526      | −0.218       |
|       | MU~Sex typicality          | −0.174     | 0.08 | −0.331      | −0.017       |
|       | MU~Asymmetry               | −0.058     | 0.078| −0.211      | 0.095        |
|       | MU~Distinctiveness         | −0.095     | 0.077| −0.246      | 0.055        |
|       | MU~BMI                     | 0.07       | 0.08 | −0.087      | 0.227        |
|       | MU~Age                     | −0.104     | 0.08 | −0.26       | 0.052        |
|       | SD residuals (sigma)       | 0.919      | 0.055| 0.82        | 1.034        |
In women, facial asymmetry and perceived attractiveness were negatively associated with morphological uniqueness (MU). Age, too, had a weak negative association with women’s MU. Distinctiveness had no association with MU. There were also positive relationships of sex typicality and BMI to MU, which indicates that morphologically feminine women and/or women with a higher BMI also have more unique facial features specific to the Cameroonian population. See Figure 2 for a bivariate relationship between MU and four indicators of biological quality in women.

![Figure 2](image-url)

**Figure 2.** A bivariate relationship between morphological uniqueness and selected predictors in women. Semitransparent corridors outline 95% compatibility intervals of counterfactual linear regression (solid line) based on 10,000 posterior samples.

In men, facial attractiveness, sex typicality, and less so age and distinctiveness were negatively associated with morphological uniqueness. Asymmetry and BMI did not reveal any conclusive unidirectional relationship with MU. See Figure 3 for bivariate relationship between MU and four target fitness indicators in men.

Then I used the thin-plate spline (TPS) interpolation function to inspect the facial features associated with Cameroonian MU (see Figure 4). Cameroonian faces with high levels of MU tend to be wider with an oval chin, the mouth characterized by massive lips with corners oriented downwards, and a shorter nose. In contrast, Cameroonian faces with low levels of MU are usually vertically prolonged, with a sharper (in men, angular) chin and a mouth with relatively thinner lips with corners oriented upwards. In faces with low levels of MU, the brows also tend to be larger than in faces with high MU. Despite some sex differences, the shape variation associated with MU is highly similar in both sexes.
Figure 3. A bivariate relationship between morphological uniqueness and selected predictors in men. Semitransparent corridors outline 95% compatibility intervals of counterfactual linear regression (solid line) based on 10,000 posterior samples.

Figure 4. Thin-plate spline visualizations of facial shape variation associated with morphological uniqueness for faces of women and men compared to the average configuration in the middle.
4. Discussion

Morphological uniqueness (MU) characterizes the relative occurrence of structurally unique formal aspects of phenotype typical of any biological group, such as members of the same population, species, or any other taxonomical category. It can be calculated as a projection of individuals sampled from the target group onto an axis connecting the target population mean with the global mean of all other samples except for the target population.

This study contrasted the faces of Cameroonian men and women with faces of people from eight other human populations spanning across four continents. When calculating the MU of Cameroonian faces, it turned out to be positively associated with several putative indicators of biological quality, and the results were different for faces of Cameroonian women and men. Female sex typicality (femininity) was positively related to MU, indicating that more feminine women are also more unique, while male sex typicality (masculinity) showed a negative relationship with MU, i.e., more masculine men were less unique. Facial asymmetry showed a strong negative association with MU in women, while for men, the association was not conclusive. Morphologically unique female faces are, thus, also the more symmetric ones. These positive associations between facial symmetry, female femininity, and MU thus seem to indicate that MU might reflect some cues of biological quality. On the other hand, the negative relationship between MU and attractiveness in both sexes (more strongly in men) indicates that MU traits are not preferred in the mate choice.

This should not lead to a premature rejection of MU as a possible indicator of the degree of ‘adaptedness’ to local conditions because attractiveness is only a weak predictor of health, fertility, and overall biological quality [46,47]. On the other hand, it is difficult to imagine that mere sex typicality without attractiveness would lead to a reproductive advantage. To properly examine the adaptiveness of MU, one should measure the actual number of children of post-reproductive individuals and correlate it with their MU levels. Alternatively, it is also possible that sex typicality can lead to greater reproductive success independently of attractiveness in traditional societies where, for instance, due to parental choice, traits other than attractiveness can play a pivotal role.

Moreover, the relation between men’s facial masculinity and their mating value is far from clear and straightforward [37,39,48–50]. It is thus possible that MU is unrelated to sexual selection but still reflects some local, perhaps environmental, adaptations. Still, the hypothesis about the adaptive role of MU is highly speculative and needs further examination. It should be noted that MU captures what is unique to a population, which does not, however, mean that such traits or features are ubiquitous or even highly common in the population in question. Faces with high levels of MU are probably perceived as somewhat extreme and therefore do not meet the general standards of beauty.

Furthermore, MU is not associated with facial distinctiveness, which also implies that it has no correlation with its logical opposite: facial averageness. That could partly explain why faces with high levels of MU are not preferred in either sex. The technical reason why standardized absolute values of MU scores tend to positively correlate with distinctiveness (Figures 2 and 3) is due to a combination of variation patterns of these two variables in the facial morphospace. While the variation of MU scores is constrained along the direction of axis connecting the target and reference groups means, distinctiveness values, represented by distances from the target group mean, may vary radially in all directions from the mean. This is why faces with a MU higher than the average have a positive association between MU and distinctiveness, while faces with a MU lower than the average exhibit a negative association between MU and distinctiveness. The closer the MU value to the Cameroonian mean, the less correlated it is with distinctiveness.

Ultimately, this independence between MU and distinctiveness may be regarded as a methodologically useful property of these two measures because they reflect two different approaches to typicality. While distinctiveness (and its opposite, averageness) captures typicality in the sense of ‘common’ traits, MU expresses the subject’s ‘exclusiveness’ in the sense of possessing characteristics unique to a particular population.
4.1. Limitations

Any measurement of morphological uniqueness is determined and therefore also limited by a shared pattern of homologies that can be defined by landmark topologies [51–53]. This means that only objects or their parts with corresponding (unequivocally homologizable) characters can be entered into a comparison. Morphologically unique structures which are not present in all members of a group—for instance, some additional appendages—are not captured by this framework.

4.2. Significance of MU for Evolutionary Studies

Current research tends to study human local adaptations largely from a genetic perspective [54–56]. This practice, however, is not optimal for furthering our understanding of the observed patterns of morphological and behavioral variation. The rapid progress in genetic methodologies and its diverse applications should not be viewed as a justification of epistemic superiority [6]. It does not mean that recent large association studies, together with transcriptomics, metabolomics, and epigenomics, do not bring relevant information about evolutionary processes [57]. However, this immense amount of information would not be meaningful without reference to a biological form and its behavioral role.

For these reasons, eco-morphological studies are essential if we want to better understand the evolution of complex organisms. The advantage of MU is that it provides a simple (unidimensional) but holistic measure based on a multivariate shape analysis to study local adaptations on the level of morphology. MU can be easily computed and used as a continuous variable which quantifies the unique morphological setup of a target group in all kinds of subsequent analyses.

Morphological uniqueness has the potential to be generalized and applied beyond the realm of human faces. Future studies may explore whether and how MU is associated with the genomic signatures of natural selection that underlies local adaptations. It can be used to explore any formal aspect of any organisms or their parts and find application within comparative biology and beyond, for instance in the study of cultural evolution of human artifacts. In theory, moreover, the concept of morphological uniqueness could be generalized and extended to additional non-shape dimensions of phenotypes, such as colors, vocalizations, or any other characteristics of living things.

Supplementary Materials: Supplementary Materials are available at https://osf.io/kqcmz/.

Funding: This research was funded by Czech Science Foundation project reg. no 21-10527S.

Institutional Review Board Statement: The study was conducted according to the guidelines of the Declaration of Helsinki, and approved by the Institutional Review Board of the Faculty of Science of the Charles University (protocol ref. number 04/2020).

Informed Consent Statement: Informed consent was obtained from all subjects involved in the study.

Data Availability Statement: All data and code are available at https://osf.io/72rbp/ (accessed on 16 November 2021).

Acknowledgments: I would like to thank to Petr Tureček for his essential help with Bayesian statistical analysis and extensive discussions on related topics. I am grateful to Ondřej Pavlovič for providing the sample of Vietnamese faces that enriched the referential facial database. I also wish to thank Anna Pilařová for English proofreading. Eventually, I thank two anonymous reviewers for their helpful comments.

Conflicts of Interest: The author declares no conflict of interest.

References

1. Lacruz, R.S.; Stringer, C.B.; Kimbel, W.H.; Wood, B.; Harvati, K.; O’Higgins, P.; Bromage, T.G.; Arsuaga, J.L. The evolutionary history of the human face. Nat. Ecol. Evol. 2019, 3, 726–736. [CrossRef]

2. Owen, R.B.; Muiruri, V.M.; Lowenstein, T.K.; Renault, R.W.; Rabideaux, N.; Luo, S.; Deino, A.L.; Sier, M.J.; Dupont-Nivet, G.; McNulty, E.P.; et al. Progressive aridification in East Africa over the last half million years and implications for human evolution. Proc. Natl. Acad. Sci. USA 2018, 115, 11174–11179. [CrossRef] [PubMed]
3. Fan, S.; Hansen, M.E.B.; Lo, Y.; Tishkoff, S.A. Going global by adapting local: A review of recent human adaptation. *Science* 2016, *354*, 54–59. [CrossRef] [PubMed]
4. Rees, J.S.; Castellano, S.; André, A.M. The Genomics of Human Local Adaptation. *Trends Genet.* 2020, *36*, 415–428. [CrossRef] [PubMed]
5. Ilardo, M.; Nielsen, R. Human adaptation to extreme environmental conditions. *Curr. Opin. Genet. Dev.* 2018, *53*, 77–82. [CrossRef]
6. Klei, K. Semantic organs: the concept and its theoretical ramifications. *Biosemiotics* 2015, *8*, 367–379. [CrossRef]
7. Muñoz, M.M.; Price, S.A. The Future is Bright for Evolutionary Morphology and Biomechanics in the Era of Big Data. *Integr. Comp. Biol.* 2019, *59*, 599–603. [CrossRef]
8. Froment, A.; Hiernaux, J. Climate-associated anthropometric variation between populations of the Niger bend. *Ann. Hum. Biol.* 1984, *11*, 189–200. [CrossRef] [PubMed]
9. Hiernaux, J. The People of Africa; Scribner: New York, NY, USA, 1975; ISBN 9780684140407.
10. Hiernaux, J.; Froment, A. The Correlations Between Anthropobiological and Climatic Variables in Sub-Saharan Africa: Revised Estimates. *Hum. Biol.* 1976, *48*, 757–767. [PubMed]
11. Hubbe, M.; Hanihara, T.; Harvati, K. Climate signatures in the morphological differentiation of worldwide modern human populations. *Anat. Rec.* 2009, *292*, 1720–1733. [CrossRef] [PubMed]
12. Zaidi, A.A.; Mattern, B.C.; Claes, P.; McEvoy, B.; Hughes, C.; Shriver, M.D. Investigating the case of human nose shape and climate adaptation. *PLoS Genetics* 2017, *13*, e1006616. [CrossRef]
13. Mariak, Z.; White, M.D.; Lewko, J.; Lyson, T.; Piekarski, P. Direct cooling of the human brain by heat loss from the upper respiratory tract. *J. Appl. Physiol.* 1999, *87*, 1609–1613. [CrossRef]
14. Maddux, S.D.; Yokley, T.R.; Svoma, B.M.; Francis, R.G. Absolute humidity and the human nose: A reanalysis of climate zones and their influence on nasal form and function. *Am. J. Phys. Anthropol.* 2016, *161*, 309–320. [CrossRef]
15. White, M.D.; Greiner, J.G.; McDonald, P.L.L. Point: Humans do demonstrate selective brain cooling during hyperthermia. *J. Appl. Physiol.* 2011, *110*, 569–571. [CrossRef] [PubMed]
16. Klei, K.; Pokorný, Š.; Čičková, M.; Froment, A.; Černý, V. Nomadic pastoralists and sedentary farmers of the Sahel/Savannah Belt of Africa in the light of geometric morphometrics based on facial portraits. *Am. J. Phys. Anthropol.* 2019, *169*, 632–645. [PubMed]
17. Matsubayashi, J.; Otsuko, K.; Morimoto, J.O.; Nakamura, F.; Nose, T.; Tayasu, I. Feeding habits may explain the morphological uniqueness of brown bears on Etorofu Island, Southern Kuril Islands in East Asia. *Biol. J. Linn. Soc.* 2016, *119*, 99–105. [CrossRef]
18. Fisher, R.A. *The Genetical Theory of Natural Selection*; Clarendon Press: Oxford, UK, 1930.
19. Hamilton, W.; Zuk, M. Heritable true fitness and bright birds: A role for parasites? *Science* 1982, 218, 384–387. [CrossRef]
20. Trivers, R.L. Parental Investment and Sexual Selection. In *Sexual Selection and the Descent of Man: The Darwinian Pivot*; Clarendon Press: Oxford, UK, 1972; pp. 136–179. ISBN 9781315129266.
21. Zahavi, A. Mate selection—a selection for a handicap. *J. Theor. Biol.* 1975, *53*, 205–214. [CrossRef]
22. Zahavi, A. The cost of honesty (further remarks on the handicap principle). *J. Theor. Biol.* 1977, 67, 603–605. [CrossRef]
23. Thornhill, R.; Gangestad, S.W. Facial attractiveness. *Trends Cogn. Sci.* 1999, *3*, 452–460. [CrossRef]
24. Van den Bergh, P.L.; Frost, P. Skin color preference, sexual dimorphism and sexual selection: A case of gene culture co-evolution? *Ethn. Racial Stud.* 1986, 9, 87–113. [CrossRef]
25. Frost, P. Human skin color: A possible relationship between its sexual dimorphism and its social perception. *Perspect. Biol. Med.* 1988, *32*, 38–58. [CrossRef] [PubMed]
26. Frost, P. European hair and eye color—A case of frequency-dependent sexual selection? *Evol. Hum. Behav.* 2006, *27*, 85–103. [CrossRef] [PubMed]
27. Fink, B.; Grammer, K.; Matts, P.J. Visible skin color distribution plays a role in the perception of age, attractiveness, and health in female faces. *Evol. Hum. Behav.* 2006, *27*, 433–442. [CrossRef]
28. Samson, N.; Fink, B.; Matts, P.J. Visible skin condition and perception of human facial appearance. *Int. J. Cosmet. Sci.* 2010, *32*, 167–184. [CrossRef] [PubMed]
29. Fink, B.; Grammer, K.; Thornhill, R. Human (Homo sapiens) facial attractiveness in relation to skin texture and color. *J. Comp. Psychol.* 2001, *115*, 92–99. [CrossRef] [PubMed]
30. Beleza, S.; dos Santos, A.M.; McEvoy, B.; Alves, I.; Martinho, C.; Cameron, E.; Shriver, M.D.; Parra, E.J.; Rocha, J. The timing of pigmentation lightening in Europeans. *Mol. Biol. Evol.* 2012, 29, 85–103. [CrossRef] [PubMed]
31. Tan, K.W.; Tiddeman, B.; Stephen, I.D. Skin texture and colour predict perceived health in Asian faces. *Evol. Hum. Behav.* 2018, *39*, 320–335. [CrossRef]
32. Saxon, T.K.; Burris, R.P.; Murray, A.K.; Rowland, H.M.; Roberts, S.C.; Craig Roberts, S. Face, body and speech cues independently predict judgments of attractiveness. *J. Evol. Psychol.* 2009, *7*, 23–35. [CrossRef]
33. Mesko, N.; Bereczkei, T. Hairstyle as an adaptive means of displaying phenotypic quality. *Hum. Nat.* 2004, *15*, 251–270. [CrossRef] [PubMed]
34. Moore, E.R.; Coetzee, V.; Contreras-Garduño, J.; Debruijne, L.M.; Klei, K.; Krams, I.; Marcinkowska, U.; Nord, A.; Perrett, D.I.; Rantala, M.J.; et al. Cross-cultural variation in women’s preferences for cues to sex- and stress-hormones in the male face. *Biol. Lett.* 2013, *9*, 20130050. [CrossRef] [PubMed]
35. Lyons, M.; Marcinkowska, U.; Moisey, V.; Harrison, N. The effects of resource availability and relationship status on women’s preference for facial masculinity in men: An eye-tracking study. *Pers. Individ. Dif.* 2016, 95, 25–28. [CrossRef]

36. Marcinkowska, U.M.; Jasienska, G.; Prokop, P. A Comparison of Masculinity Facial Preference Among Naturally Cycling, Pregnant, Lactating, and Post-Menopausal Women. *Arch. Sex. Behav.* 2018, 47, 1367–1374. [CrossRef] [PubMed]

37. Marcinkowska, U.M.; Rantala, M.J.; Lee, A.J.; Kozlov, M.V.; Aavik, T.; Cai, H.; Contreras-Garduño, J.; David, O.A.; Kaminski, G.; Li, N.P.; et al. Women’s preferences for men’s facial masculinity are strongest under favorable ecological conditions. *Sci. Rep.* 2019, 9, 3387. [CrossRef] [PubMed]

38. Johnston, V.S.; Hagel, R.; Franklin, M.; Fink, B.; Grammer, K. Male facial attractiveness: Evidence for hormone-mediated adaptive design. *Evol. Hum. Behav.* 2001, 22, 251–267. [CrossRef]

39. Kleisner, K.; Tureček, P.; Roberts, S.C.; Havlíček, J.; Valentova, J.V.; Akoko, R.M.; Leongómez, J.D.; Apostol, S.; Varella, M.A.C.; Saribay, S.A. How and why patterns of sexual dimorphism in human faces vary across the world. *Sci. Rep.* 2021, 11, 5978. [CrossRef] [PubMed]

40. Adams, D.C.; Collyer, M.L.; Kaliontzopoulou, A. Geomorph: Software for geometric Morphometric Analyses. R Package Version 3.1.0. 2019. Available online: https://cran.r-project.org/web/packages/geomorph/index.html (accessed on 20 August 2021).

41. Adams, D.C.; Otárola-Castillo, E. geomorph: An R package for the collection and analysis of geometric morphometric shape data. *Methods Ecol. Evol.* 2013, 4, 393–399. [CrossRef]

42. Schlager, S. Morpho and Rv Gaussian—Shape Analysis in R: R-Packages for Geometric Morphometrics, Shape Analysis and Surface Manipulations. In *Statistical Shape and Deformation Analysis*; Zheng, G., Li, S., Székely, G., Eds.; Academic Press: Cambridge, MA, USA, 2017; pp. 217–256. ISBN 978-0-12-810493-4.

43. Zelditch, M.L.; Swiderski, D.L.; Sheets, H.D. *Geometric Morphometrics for Biologists*, 2nd ed.; Academic Press: San Diego, CA, USA, 2012; ISBN 978-0-12-386903-6.

44. McElreath, R. *Rethinking: Statistical Rethinking* Book Package Version 1.59 from GitHub 2020. Available online: https://github.com/rmcelreath/rethinking (accessed on 20 August 2021).

45. Stan Development Team. *RStan: The R interface to Stan*. R Package Version 2.21.2. Available online: https://mc-stan.org/ (accessed on 20 August 2021).

46. Foo, Y.Z.; Simmons, L.W.; Rhodes, G. Predictors of facial attractiveness and health in humans. *Sci. Rep.* 2017, 6, 39731. [CrossRef]

47. Jokela, M. Physical attractiveness and reproductive success in humans: Evidence from the late 20th century United States. *Evol. Hum. Behav.* 2013, 34, 302–311. [CrossRef] [PubMed]

48. Fiala, V.; Trehický, V.; Pázhoohi, F.; Leongómez, J.D.; Tureček, P.; Saribay, S.A.; Akoko, R.M.; Kleisner, K. Facial attractiveness and preference of sexual dimorphism: A comparison across five populations. *Evol. Hum. Sci.* 2021, 3, e38. [CrossRef]

49. Zaidi, A.A.; White, J.D.; Mattern, B.C.; Liebowitz, C.R.; Puts, D.A.; Claes, P.; Shriver, M.D. Facial masculinity does not appear to be a condition-dependent male ornament and does not reflect MHC heterozygosity in humans. *Proc. Natl. Acad. Sci. USA* 2019, 116, 1633–1638. [CrossRef] [PubMed]

50. Boothroyd, L.G.; Gray, A.W.; Headland, T.N.; Uehara, R.T.; Waynforth, D.; Burt, D.M.; Pound, N. Male Facial Appearance and Offspring Mortality in Two Traditional Societies. *PLoS ONE* 2017, 12, e0169181. [CrossRef]

51. Kleisner, K. The formation of the theory of homology in biological sciences. *Acta Biobiol.* 2007, 55, 317–340. [CrossRef]

52. Wärmländer, S.K.T.S.; Garvin, H.; Guyomarc’h, P.; Petaros, A.; Sholts, S.B. Landmark Typology in Applied Morphometrics Studies: What’s the Point? *Anat. Rec.* 2019, 302, 1144–1153. [CrossRef] [PubMed]

53. Books, F.L. *Morphometric tools for Landmark Data: Geometry and Biology*; Cambridge University Press: Cambridge, UK, 1997.

54. Fraser, H.B. Gene expression drives local adaptation in humans. *Hum. Genet.* 2013, 317–340. [CrossRef]

55. Key, F.M.; Fu, Q.; Romagné, F.; Lachmann, M.; Andrés, A.M. Human adaptation and population differentiation in the light of ancient genomes. *Nat. Commun.* 2016, 7, 10775. [CrossRef] [PubMed]

56. Bergström, A.; McCarthy, S.A.; Hui, R.; Almarri, M.A.; Ayub, Q.; Danecek, P.; Chen, Y.; Felkel, S.; Hallast, P.; Kamn, J.; et al. Insights into human genetic variation and population history from 929 diverse genomes. *Science* 2020, 367, eaay5012. [CrossRef] [PubMed]

57. Akiyama, M. Multi-omics study for interpretation of genome-wide association study. *J. Hum. Genet.* 2021, 66, 3–10. [CrossRef] [PubMed]