Is Homo sapiens polytypic? Human taxonomic diversity and its implications

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SUMMARY

The term race is a traditional synonym for subspecies, however it is frequently asserted that Homo sapiens is monotypic and that what are termed races are nothing more than biological illusions. In this manuscript a case is made for the hypothesis that H. sapiens is polytypic, and in this way is no different from other species exhibiting similar levels of genetic and morphological diversity. First it is demonstrated that the four major definitions of race/subspecies can be shown to be synonymous within the context of the framework of race as a correlation structure of traits. Next the issue of taxonomic classification is considered where it is demonstrated that H. sapiens possesses high levels morphological diversity, genetic heterozygosity and differentiation (F_{ST}) compared to many species that are acknowledged to be polytypic with respect to subspecies. Racial variation is then evaluated in light of the phylogenetic species concept, where it is suggested that the least inclusive monophyletic units exist below the level of species within H. sapiens indicating the existence of a number of potential human phylogenetic species; and the biological species concept, where it is determined that racial variation is too small to represent differentiation at the level of biological species. Finally the implications of this are discussed in the context of anthropology where an accurate picture of the sequence and timing of events during the evolution of human taxa are required for a complete picture of human evolution, and medicine, where a greater appreciation of the role played by human taxonomic differences in disease susceptibility and treatment responsiveness will save lives in the future.

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Introduction

Historically, the term race has been used in biology as a synonym for subspecies [1,2]. Whereas the term subspecies was typically used in the description of infra-specific diversity in non-human animal species, the term 'race' tends to be employed exclusively in the description of diversity present within the human species. Despite this it is frequently asserted that humans are monotypic (belonging to one species and one subspecies – Homo sapiens sapiens), and that 'racial' diversity is either a socially constructed biological illusion or that it exists only at infra-subspecific scales and is therefore taxonomically trivial. In this manuscript a case will be made for the hypothesis that H. sapiens in fact polytypic and that this has significant implications for fields such as anthropology and medicine.

Conceptions of race

Four major definitions of what constitutes a subspecies or race have been identified by Long and Kittles [3].

Table 1 illustrates the evolution of classificatory concepts of race from essentialist to lineage based. Although in each case the idea of 'distinctness' is invoked as a necessary criterion for the existence of a race there exists considerable disagreement over how to define that distinctness. The essentialist concept of Hooton places the emphasis on the existence of combinations of characteristics shared through common descent, whereas the taxonomic concept uses a combination of phenotypic similarity coupled with the idea of range restriction. The population concept of Dobzhansky on the other hand talks of race exclusively in terms of Mendelian populations whilst the lineage concept of Templeton requires races to have been subject to historical barriers to gene flow whilst simultaneously exhibiting contemporary genetic differentiation.

Social constructivism

The table would seem to suggest that there is no universally agreed upon definition of race or subspecies and that the use of any particular race concept in the apportionment of human biological diversity is to a degree arbitrary. This situation has not been helped by inconsistent historical usage in the anthropological literature, where the term would frequently be used in the description of human populations at a variety of scales ranging from sub-continental to global [7].
This suggestion of arbitrariness has led many social scientists to claim that what is termed ‘race’ is in fact nothing more than a ‘social-construct’, devoid of any biological foundation. According to this view, which is known generally as social constructivism, the concept of racial classification is a recent invention (c. 18th century) and was developed as a means of grouping subjugated colonial peoples on the basis of arbitrary physical characteristics. By this logic the very notion of race therefore has inherently racist connotations as, it is inferred, the decision to use concepts of race in the ‘arbitrary’ grouping of humans is suggestive of a desire to delineate an out-group that is some way ‘inferior’ in contradistinction to a ‘superior’ in-group to which, it is presumed, the classifier would belong [8,9]. As evidence of the pervasiveness of the view that races do not exist within the social sciences, a 1985 survey of 1200 academics who were asked whether they disagreed with the statement: “There are biological races in the species Homo sapiens”, revealed that only 16% of biologists disagreed as compared to 53% of socio-cultural anthropologists [10]. The likelihood is that an even higher percentage of social scientists would disagree today. As evidence of this, one only needs to read the official position statements on race and ethnicity of major organizations such as the American Anthropological Association and the American Sociological Association.

The problem with social constructivism is that it attempts to engage racial classification on a normative rather than a scientific level. Using the idea that scientific race concepts stem from a desire to apportion people into ‘inferior’ vs. ‘superior’ categories as grounds for claiming that they are wrong is simply an appeal to motive and therefore is not a logical counter to scientific theories of race, which must be assessed purely on their merits. The notion of arbitrariness in the definition of race is a significant and legitimate scientific issue in need of redress however.

Defining race

Prior to examining the race concept from a classificatory standpoint it is necessary to demonstrate its validity as a biological construct independently of classificatory schemes. It was mentioned previously that all four of the major race concepts require races to be in some way distinct from one another, however it is frequently asserted that because the majority of genetic variation (85%) lies within the classically defined racial groups rather than between them (some estimates indicate that the number is as low as 6%), race is therefore a taxonomically meaningless category. Lewontin, who is the most influential proponent of this hypothesis, essentially assumed that because there is a 30% probability of misclassifying an individual’s race based on the variation in a single genetic locus, race must therefore be taxonomically invalid [11]. Lewontin’s claim was essentially a formalization of the old argument that human populations are too clinal (they share too much variance) to be clearly differentiable into races [12,13]. Edwards

<table>
<thead>
<tr>
<th>Concept</th>
<th>Definition</th>
<th>Author(s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Essentialist</td>
<td>A significant division of the human species, they are characterized through shared combinations of traits derived through common descent. They constitute a vague physical background, obscured to a degree by individual variations, best realizable as composites</td>
<td>Hooton [4]</td>
</tr>
<tr>
<td>Taxonomic</td>
<td>Aggregate populations of a species possessing phenotypic similarities and inhabiting geographic subdivisions of the range of the species. They differ taxonomically amongst themselves</td>
<td>Mayr [5]</td>
</tr>
<tr>
<td>Population</td>
<td>Genetically distinct Mendelian populations. Neither individuals nor specific genotypes, they consist of genetically differentiated individuals</td>
<td>Dobzhansky [6]</td>
</tr>
<tr>
<td>Lineage</td>
<td>Distinct evolutionary lineages within species exhibiting historical continuity owing to the operation of persistent, long-term barriers to genetic exchange, which have resulted in their having become genetically differentiated</td>
<td>Templeton [1]</td>
</tr>
</tbody>
</table>

![Fig. 1. A graph illustrating the so-called ‘Lewontin's fallacy’](http://www.gnxp.com, creative commons licensed).
tinct correlation structures could not have been subject to historical restrictions in gene flow, as is required by the lineage definition of Templeton. These last two would in point of fact be a prerequisite for the evolution of racial differences in the first instance. The four major race concepts can therefore be united within a common descriptive framework, the differences between them are purely a matter of where the descriptive emphasis is placed.

Races as biological subspecies

Demonstrating the biological construct validity of race does not necessarily address the issue of classification. Although it has been shown that the four major approaches at defining race differ only in terms of qualitative descriptive expression, the problem of taxonomic arbitrariness in terms of how diversity within species is classified is still an issue.

An old morphological method for determining the appropriateness of a subspecies classification is the 75% rule, which holds that if 75% of the members of a given population can be grouped by eye then they constitute a subspecies [15]. Although there is debate about its utility today [16], it has been observed that individual humans can accurately be grouped based on race more than 75% of the time [17], which contrasts sharply with chimpanzees whose four recognized subspecies are extremely difficult to differentiate through visual inspection [18]. It has also been noted that morphological differences among humans are not only on average about equal to the distances among species within other genera of mammals (with the exception of populations generated under domestication pressures, such as breeds of dog) but are typically more strongly marked than in other animals [9].

It must be noted however that small genetic differences can give rise to sharp morphological differences through pleiotropy, a good example of this being dog breeds, which are not considered to be separate subspecies; so to illustrate the inconsistency with which race and synonymous concepts have been used in the classification of infra-specific diversity at molecular levels, comparative measures of genetic diversity based on allele frequency data (heterozygosity) for a range of species along with the numbers of recognized extant subspecies are presented in the following table.

**Table 2**

<table>
<thead>
<tr>
<th>Species (vernacular name)</th>
<th>$H_e$</th>
<th>$H_o$</th>
<th>Number of recognized extant subspecies</th>
<th>Author(s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Humans</td>
<td>–</td>
<td>0.776</td>
<td>1</td>
<td>Wise et al. [20]</td>
</tr>
<tr>
<td>Humans</td>
<td>–</td>
<td>0.7–0.76</td>
<td>1</td>
<td>Jorde et al. [21]</td>
</tr>
<tr>
<td>Humans</td>
<td>–</td>
<td>0.588–0.807</td>
<td>1</td>
<td>Bowcock et al. [22]</td>
</tr>
<tr>
<td>Chimpanzees</td>
<td>0.78</td>
<td>0.73</td>
<td>4</td>
<td>Reinartz et al. [23]</td>
</tr>
<tr>
<td>Chimpanzees</td>
<td>0.63</td>
<td>0.48</td>
<td>1</td>
<td>Wise et al. [20]</td>
</tr>
<tr>
<td>Bonobos</td>
<td>0.59</td>
<td>0.48</td>
<td>1</td>
<td>Reinartz et al. [23]</td>
</tr>
<tr>
<td>African buffalo</td>
<td>0.759</td>
<td>0.729</td>
<td>5</td>
<td>Van Hooff et al. [24]</td>
</tr>
<tr>
<td>Leopards</td>
<td>0.36–0.8</td>
<td>–</td>
<td>Between 8 and 18 depending on the preferred taxonomy</td>
<td>Uphyrkina et al. [25]</td>
</tr>
<tr>
<td>Jaguars</td>
<td>0.739</td>
<td>–</td>
<td>9</td>
<td>Ezirik et al. [26]</td>
</tr>
<tr>
<td>Pumas</td>
<td>–</td>
<td>0.52</td>
<td>6</td>
<td>Culver et al. [27]</td>
</tr>
<tr>
<td>Canadian lynx</td>
<td>–</td>
<td>0.66</td>
<td>3</td>
<td>Schwartz et al. [28]</td>
</tr>
<tr>
<td>Polar bears</td>
<td>0.68</td>
<td>–</td>
<td>1</td>
<td>Paetkau et al. [29]</td>
</tr>
<tr>
<td>Brown bears (N. America)</td>
<td>0.26–0.76</td>
<td>0.3–0.79</td>
<td>19</td>
<td>Paetkau et al. [30]</td>
</tr>
<tr>
<td>Brown bears (Scandinavia)</td>
<td>0.709</td>
<td>0.665</td>
<td>19</td>
<td>Waits et al. [31]</td>
</tr>
<tr>
<td>Coyote</td>
<td>0.675</td>
<td>0.583</td>
<td>19</td>
<td>Garcia-Moreno et al. [32]</td>
</tr>
<tr>
<td>Gray wolf (N. America)</td>
<td>0.62</td>
<td>0.528</td>
<td>37</td>
<td>Garcia-Moreno et al. [32]</td>
</tr>
<tr>
<td>Dogs (42 breeds)</td>
<td>0.616</td>
<td>0.401</td>
<td>1</td>
<td>Garcia-Moreno et al. [32]</td>
</tr>
<tr>
<td>African wild dogs</td>
<td>0.643</td>
<td>–</td>
<td>5</td>
<td>Gimran et al. [33]</td>
</tr>
<tr>
<td>Dingo</td>
<td>0.47</td>
<td>0.42</td>
<td>1</td>
<td>Wilton et al. [34]</td>
</tr>
<tr>
<td>Wolverines (N. America)</td>
<td>0.42–0.68</td>
<td>–</td>
<td>Between 2 and 3 depending on the preferred taxonomy</td>
<td>Kyle and Strobeck [35]</td>
</tr>
<tr>
<td>Wolverines (Scandinavia)</td>
<td>–</td>
<td>0.27–0.38</td>
<td>–</td>
<td>Walker et al. [36]</td>
</tr>
<tr>
<td>Elk (N. America)</td>
<td>0.26–0.53</td>
<td>–</td>
<td>Between 7 and 8 depending on the preferred taxonomy</td>
<td>Polzieln et al. [37]</td>
</tr>
<tr>
<td>Bighorn sheep</td>
<td>0.681</td>
<td>0.566</td>
<td>3</td>
<td>Forbes et al. [38]</td>
</tr>
</tbody>
</table>

Based on Table 2, it is evident that the ‘*H. sapiens*’ as monotypic species’ theory is inconsistent with the way in which taxonomic classification has been employed for other species exhibiting similar degrees of heterozygosity. Chimpanzees for example exhibit very similar degrees of observed heterozygosity to humans (0.63–0.73 vs. 0.588–0.807) yet have been divided into four subspecies. Some species such as the grey wolf actually exhibit lower levels of observed heterozygosity than humans (0.528 vs. 0.588–0.807) yet have been divided into as many as 37 subspecies. When measures of genetic distance are used such as Wright's $F_{ST}$, which describes the fraction of the variation attributable to population subdivision, values indicative of great levels of genetic differentiation have been obtained for humans (0.156) based on the analysis of autosomal loci [39] (great levels of genetic differentiation correspond to values of between 0.15 and 0.25 [40]). This contrasts with scores indicative of little to moderate levels of genetic differentiation in other animals (again obtained by looking at autosomal loci), such as the Canadian lynx (0.033) [28], which is recognized as having three subspecies, and the African buffalo (0.059) [24], which is recognized as having five subspecies. A relevant question to ask at this stage is how many subspecies comprise *H. sapiens*?

Traditionally, anthropologists have recognized four great races on morphological grounds (Cordoid or ‘Negr oid’, Caucasoid, Mongoloid and Australoid) with Capoid (SE Africans) sometimes described as a fifth [41]. Molecular data have resulted in this structure being modified slightly with the analysis of classical and other genetic markers consistently revealing the presence of around five continental populations (major clades or races) in the form of Sub-Saharan Africans, Caucasians (European and Non-European), NE (Greater) Asians, SE Asians and Pacific Islanders (includes Australo-papuans) and Amerindians [42–45]. Subspecies identified cladistically not only compliment the definition of race as correlation structure, but also present an adequate solution to the problem of arbitrariness in traditional taxonomic approaches to the classification of human racial diversity [45,46].

Are there multiple extant human species?

A minority of anthropologists in the past have held the view that human racial morphological differences are great enough in
some instances to warrant being considered as species level differences [47]; however these views were often based upon the use of scientifically inappropriate morphological comparisons with extant primates (such as degree of prognathism). In this section, the two major definitions of species will be considered in addressing this question.

Species concepts

As with the concept of race, there have been multiple attempts made at defining species. There are around 14 different species concepts, however as far as vertebrate classification is concerned, there are currently two major classification paradigms: the traditional biological species concept and the phylogenetic species concept, which also happen to be amongst the most diametrically different of the species concepts.

Table 3 illustrates the differences between the biological species concept of Mayr, which regards species as the end products of an evolutionary chain of events that have lead to the establishment of reproductively isolated populations; and the phylogenetic species concept, first introduced by Eldridge and Crockart, which sees species as being defined in terms of the evolutionary distinctiveness of lineages. A number of alternative definitions of phylogenetic species can have been proposed. Eldridge and Crockart saw synapomorphic characteristics (shared characteristics derived from a common ancestor) as the unit that both united and defined the smallest aggregate population or lineage, in other words the synapomorphic species [48]. Mishler and Theriot have however suggested that the phylogenetic species is in fact that least inclusive taxon in a formal phylogenetic classification [49]. The various phylogenetic species concepts can ultimately be shown to be highly similar, they also explicitly reject the existence of subspecies as a valid level of classification.

Table 3

The biological and phylogenetic species concepts.

<table>
<thead>
<tr>
<th>Concept</th>
<th>Definition</th>
<th>Author(s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phylogenetic</td>
<td>Species are the result of clear divergence within a group of organisms sharing an ancestor whose lineage remains intact with respect to other lineages throughout time and space. Subspecies are not recognized.</td>
<td>Eldridge and Crockart [48]</td>
</tr>
<tr>
<td>Biological</td>
<td>Species are comprised of populations that either have the potential to or actually interbreed, and are reproductively isolated from other such populations</td>
<td>Mayr [5]</td>
</tr>
</tbody>
</table>

Races as phylogenetic species

A valid question to ask is what are human races in terms of the phylogenetic species concept? It has been suggested by Platnick and Wheeler [50] that prior to the advent of intercontinental travel, character distributions would have suggested the existence of more than one phylogenetic species of human, however high levels of interbreeding in recent years have effectively negated the evolutionary distinctiveness of human populations to the point where they are currently no longer diagnostically as species. This can be countered with the observation that admixture between racial groups seems to be less common than Platnick and Wheeler assume. Even when racial groups are living in close proximity to one another, the likelihood of admixture has been observed to be a function of the degree of genetic similarity between racial groups, indicating that mate preferences restrict large-scale admixture [51–53]. The implication of this is that racial and sub-racial populations likely continue to remain distinct enough, despite increases in demographic mobility, to make them still potentially diagnosable as phylogenetic species.

As phylogenetic species represent the least inclusive monophyletic taxonomic unit within classical taxonomic schemes, the concept dispenses with hierarchical classification altogether. Based on this classification, there exist only phylogenetic species grouped based on shared synapomorphic characteristics. If the sub-continental (sub-racial) populations identified by Cavalli-Sforza [43,44] are used as the least inclusive monophyletic grouping, then there could be around 38 extant phylogenetic species comprising humanity, although it is not inconceivable that there may be many more as phylogenetic species need only theoretically differ from one another by as little as a single base in order for them to be considered as having the potential to assume unique evolutionary trajectories.

Are there unrecognized biological species within Homo?

Sarich and Meile have suggested that racial differences in craniofacial morphology are typically around 10 times the corresponding differences between the sexes within a given race, which they note, is larger than the comparable differences that taxonomists use in distinguishing common chimpanzees from bonobos [9], however phenetics provide a poor basis for differentiating between biological species owing to the highly pleiotropic effects that small genetic differences can have on morphology.

Fuerle has recently attempted to build a case for the existence of multiple biological species of humans from a molecular perspective. Fuerle used comparative genetic distance data involving various DNA types obtained from a variety of sources for a range of biological species and subspecies [54]. The results of his review are summarized in the following table. Additional data involving non-mtDNA based estimates of the genetic distance between the gorilla species and the chimpanzees and bonobos have been included for comparison.

Table 4 would seem to suggest that the Sub-Saharan African (Bantu) and Australopapuan (Aborigine) genetic difference as measured by SNP’s is greater than the genetic distance between both the two species of gorilla (Gorilla gorilla and Gorilla beringei), and greater than the distance between the common chimpanzee and the bonobo as measured by mtDNA.

On the basis of this Fuerle suggests that there are only two consistent courses of action to take regarding re-classification – splitting or lumping. Either Homo sapiens could be split into two species – Homo africanus which would encompass modern African populations and Homo eurasiensis which would encompass Eurasian populations; making the genus Homo consistent in his view, species-wise with respect to other genera in which the differences between species are expressed in much smaller genetic distances; or alternatively the genetic variability within the human species could be used to typologically define the absolute limits of what constitutes a vertebrate species, which could then be employed as a taxonomic baseline in the classification of other species. This would mean lumping the two gorilla species and the chimpanzee and the bonobo as single species.

Criticisms of Fuerle’s arguments

$F_{ST}$ reflects the relative amount of total genetic differentiation between populations, however different measures of genetic distance involving mtDNA and autosomal loci are simply inappropri-
ate for the purposes of inter-specific comparison as the different genes involved will have been subject to markedly different selection pressures and are therefore not likely to have diverged at the same time [62]. To illustrate this point, this author listed alternative estimates of the distance between the gorilla species and the common chimpanzee and bonobo, based on various nuclear loci and autosomal DNA. The much higher numbers reflect the extreme variation that can be expected when different genes are considered. Fuerle's presentation of the data is also problematic for another reason, namely he makes no mention of the current debates surrounding gorilla and chimpanzee/bonobo taxonomy: as new research on these taxa regularly generates novel and in some cases wildly variable estimates of genetic distance between these primates, and there is even some debate over whether the eastern and western gorillas are separate species [60].

Curnoe and Thorne have estimated that periods of around two million years were required for the production of sufficient genetic distances to represent speciation within the human ancestral lineage [56]. This indicates that the genetic distances between the races are too small to warrant differentiation at the level of biological species, as the evolution of racial variation within H. sapiens started to occur only 60,000 years ago, when the ancestors of modern humans first left Africa.

Discussion

Overview of findings

There are strong grounds for suggesting that the hypothesis that H. sapiens is polytypic rather than monotypic is at least plausible: this argument is based upon the following lines of reasoning. Firstly, it has been demonstrated that there exists a considerable degree of diversity (as measured by morphology, heterozygosity and FST) within this taxon, which is structured in such a way that is suggestive of the existence of around five major clades (continental populations) corresponding to biological subspecies. And secondly, as the phylogenetic species concept does not recognize the validity of subspecies as a division, opting instead to label these primates, and there is even some debate over whether the eastern and western gorillas are separate species [60].

Curnoe and Thorne have estimated that periods of around two million years were required for the production of sufficient genetic distances to represent speciation within the human ancestral lineage [56]. This indicates that the genetic distances between the races are too small to warrant differentiation at the level of biological species, as the evolution of racial variation within H. sapiens started to occur only 60,000 years ago, when the ancestors of modern humans first left Africa.

jor racial groups within H. sapiens are greater than the distances recorded between certain other primate species; collapse on the basis that such comparisons have been made by inaccurately comparing FST estimates derived for different gene-types with different potential selection histories.

Implications of the hypothesis

Palaeoanthropologists in the ‘splitting’ tradition seem only too willing to argue the case for each new fossil hominin find being a unique species, however these same researchers seem reluctant to suggest that contemporary humanity may abound in taxonomic diversity. This is of course understandable in light of the fact that the issue of race is often a politically incendiary one and researchers who wish to maintain their careers and reputations tend to stay well away from it [63], but is it necessarily wise to ignore the reality of human taxonomic diversity?

There exists to the mind of this author, two salient reasons why the recognition of new extant human taxa is desirable. Firstly, it would appear that those who insist on ‘lumping’ human taxonomic diversity into a single monotypic species are making a specific claim about the evolutionary relationships and distinguishability of members of that group – namely that only the overarching similarities between human groups matter from the perspective of classification. This holism is however detrimental to a consistent understanding of recent human evolution as only through full consideration of the timing and causes of the points of divergence between the major taxa of humanity can an entirely accurate model of human evolution be devised.

Secondly, within medicine, knowledge of a patient’s racial and ethnic background is often a significant factor in the appropriate selection of treatment modalities. It is well known for example that the survival rates of transplant patients are influenced by race, as the lack of close ethnic matching between donor and patient is a significant factor influencing tissue rejection [64,65]. Many diseases are known to differentially affect racial and ethnic groups. Melanoma has a higher incidence in Caucasians than in any other racial group, Tay Sachs disease predomately affects people of the Ashkenazi Jewish ethnicity, sickle cell anaemia is extraordinarily rare in people of non-African ancestry, even factors such as tolerance to alcohol, the likelihood of developing heart disease, hypertension and their responsiveness to medication can be partly predicted based on racial data [66]. The list is long and is illustrative of the fact that the assumption that racial differences are meaningful biologically is important to medicine, both to the research and practice aspects of it.

Medical ethicists seem to be becoming increasingly sympathetic to the arguments of the social constructivists however...
[67,68], there also appears to be growing support for the extension of current regulations on the use of race in biomedical research [69,70] which is an especially alarming trend as a medical ethics and to medical progress in general in the post-genomics era.

Conflicts of interest statement
None declared.

References