

Is *Homo sapiens* polytypic? Human taxonomic diversity and its implications

Michael A. Woodley*

School of Biological Sciences, Royal Holloway, University of London, Egham, Surrey, UK

ARTICLE INFO

Article history:

Received 20 July 2009

Accepted 22 July 2009

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* is 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].

* Address: Highfield Court, Highfield Road, Building 3, Apt. 3256, Surrey, Egham, TW200TB, UK. Tel.: +44 07717 643 658.

E-mail address: M.A.Woodley@rhul.ac.uk

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].

Table 1
The four major definitions of race/subspecies.

Concept	Definition	Author(s)
Essentialist	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	Hooton [4]
Taxonomic	Aggregate populations of a species possessing phenotypic similarities and inhabiting geographic subdivisions of the range of the species. They differ taxonomically amongst themselves	Mayr [5]
Population	Genetically distinct Mendelian populations. Neither individuals nor specific genotypes, they consist of genetically differentiated individuals	Dobzhansky [6]
Lineage	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	Templeton [1]

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 *H. 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 stand point 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 promoter 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

has however countered these arguments with the observation that although Lewontin and others are correct when talking about a single locus or trait, concluding from this that race does not exist is fallacious as the likelihood of not being able to differentiate between racial groups rapidly approaches 0% as more loci or traits are considered. This is due to the fact that loci/trait frequencies within racial groups tend to be correlated [14].

Based on Fig. 1, race and synonymous concepts can be defined as populations expressing a composite number of traits whose distributions intercorrelate in such a way so as to give rise to a particular, distinct correlative structure. This basic definition allows for a potential reconciliation of the four major attempts at defining race listed in Table 1. Hooton's essentialist definition, which requires the sharing of characteristics through common descent is clearly compatible with the observation that race is a correlation structure of traits, as is Mayr's taxonomic definition, which sees races as phenotypically similar groups occupying different ranges. Eco-geographical distinctions between races would be to a degree congruent with respect to genetic and phenotypic traits, so would be expected to yield correlation structures similar to Fig. 1.

There is no reason why such correlation structures could not correspond to Mendelian populations as is required by the population definition of Dobzhansky, nor is there any reason why the dis-

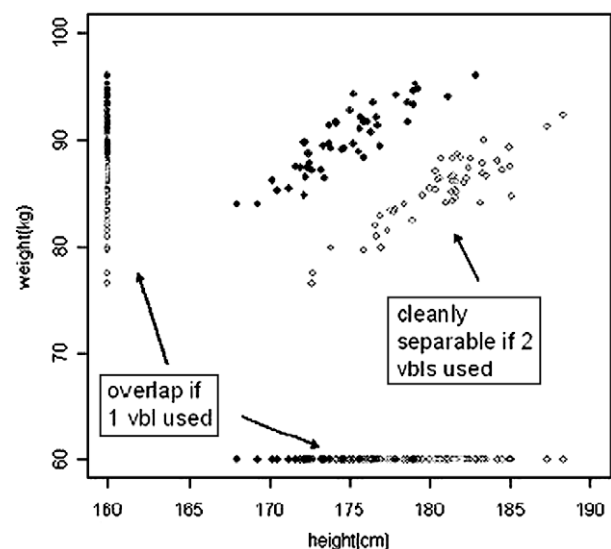


Fig. 1. A graph illustrating the so-called 'Lewontin's fallacy'. In this example there are two hypothetical races (black and white points) defined by different combinations and distributions of weight and height. If information about only a single variable (analogous to a genetic locus) is used to identify a race then the identity is partially obscured as a result of overlap. If information about two variables is considered however, races emerge as cleanly separable and distinct clusters (image retrieved and modified from <http://www.gnpx.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 attempts at defining race differ only in terms of qualitative descriptive emphasis, 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

Comparative values of genetic diversity for a variety of mammalian species representatively sampled across their respective ranges (except where indicated), as measured by autosomal microsatellites (H_e = expected heterozygosity; H_o = observed heterozygosity). Data listed in Goodrum [19] and other sources.

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

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 (Congoid or ‘Negroid’, 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 Australopapuan) 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 Cracraft, which sees species as being defined in terms of the evolutionary distinctiveness of lineages. A number of alternative definitions of phylogenetic species have been proposed. Eldridge and Cracraft 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 phylogenetic 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.

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 diagnosable 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 con-

cept 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 *H. sapiens* could be split into two species – *Homo africanus* which would encompass modern African populations and *Homo eurasianensis* 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 terms of 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-

Table 3
The biological and phylogenetic species concepts.

Concept	Definition	Author(s)
Phylogenetic	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	Eldridge and Cracraft [48]
Biological	Species are comprised of populations that either have the potential to or actually interbreed, and are reproductively isolated from other such populations	Mayr [5]

Table 4Comparative pair-wise genetic distances (expressed in terms of F_{ST}) between various biological species (and subspecies) as listed in Fuerle [54] and other sources.

Species (vernacular names)	Species (scientific names)	Genetic distance	DNA type	Author(s)
Sub-Saharan African (Bantu) vs. Australopapuan (Aborigine)	<i>H. sapiens</i>	0.33	Single nucleotide polymorphism(SNP)	Salter [52]
Sub-Saharan African (Bantu) vs. Eurasian (English)	<i>H. sapiens</i>	0.24	SNP	Salter [52]
Human vs. Neanderthal	<i>H. sapiens sapiens, Homo neanderthalensis</i>	<0.08	mtDNA	Caramelli et al. [55]; Curnoe and Thorne [56]; Gutiérrez et al. [57]
Human vs. <i>Homo erectus</i>	<i>H. sapiens, Homo erectus</i>	0.17	mtDNA (inferred)	Curnoe and Thorne [56]
Western gorilla vs. Eastern gorilla	<i>Gorilla gorilla, Gorilla beringei</i>	0.02–0.29	mtDNA	Jensen-Seaman [58]; Guillén et al. [59]
Western gorilla vs. Eastern gorilla	<i>Gorilla gorilla, Gorilla beringei</i>	0.38	14 nuclear loci	Thalmann et al. [60]
Common chimpanzee vs. Bonobo	<i>Pan troglodytes, Pan paniscus</i>	0.05–0.2	mtDNA	Guillén et al. [59]
Common chimpanzee vs. Bonobo	<i>Pan troglodytes, Pan paniscus</i>	0.49–0.68	Autosomal DNA	Becquet et al. [61]

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 F_{ST}) 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 the most basic monophyletic unit as 'species', a case could be made for the minor clades (sub-continental/racial populations) within *Homo* qualifying as phylogenetic species in their own right, especially when considered in light of the evidence suggestive of the idea that lineage admixture is in fact fairly peripheral and is probably not negating the evolutionary distinctiveness of those groups. No substantial evidence exists in favour of the idea that there are multiple human biological species however. Arguments based on the use of comparative genetic distances between biological species that are suggestive of the idea that the distances between ma-

ior 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 incautiously comparing F_{ST} 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 hominid 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 predominately 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, hypotension 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 that broadly rejects the biological reality of race will surely pose a formidable obstacle to the realization of personalized medicine and to medical progress in general in the post-genomics era.

Conflicts of interest statement

None declared.

References

- [1] Templeton AR. Human races: A genetic and evolutionary perspective. *Am Anthropol* 1998;100:632–50.
- [2] Bodmer WF, Cavalli-Sforza LL. Genetics, evolution, and man. San Francisco, CA, USA: WH Freeman and Company; 1976.
- [3] Long JC, Kittles RA. Human genetic diversity and the nonexistence of biological races. *Hum Biol* 2003;75:449–71.
- [4] Hooton EA. Methods of racial analysis. *Science* 1926;63:75–81.
- [5] Mayr E. Principles of systematic zoology. New York, NY, USA: McGraw-Hill; 1969.
- [6] Dobzhansky T. Genetics of the evolutionary process. New York, NY, USA: Columbia University Press; 1970.
- [7] Strkalj G. Form and race. Terminological concepts for the study of human variation. *Mankind Q* 2000;41:109–18.
- [8] Mills CW. Blackness visible: Essays on philosophy and race. Ithaca, NY, USA: Cornell University Press; 1998.
- [9] Sarich V, Miele F. Race: the reality of human differences. New York, NY, USA: Westview Press; 2004.
- [10] Leiberman L, Hampton RE, Littlefield A, Hallead G. Race in biology and anthropology: A study of college texts and professors. *J Res Sci Teach* 1992;29:301–21.
- [11] Lewontin RC. The apportionment of human diversity. *Evol Biol* 1972;6:381–97.
- [12] Brace CL. On the race concept. *Curr Anthropol* 1964;5:313–20.
- [13] Brace CL. A non-racial approach towards the understanding of human diversity. In: Montagu MFA, editor. The concept of race. New York, NY, USA: Free Press of Glencoe; 1964.
- [14] Edwards AWF. Human genetic diversity: Lewontin's fallacy. *Bioessays* 2003;25:798–801.
- [15] Amadon D. The seventy-five percent rule for subspecies. *Condor* 1949;51:251–8.
- [16] Smith H, Chiszer D, Montanucci R. Subspecies and classification. *Herp Rev* 1997;28:13–6.
- [17] Wright S. Evolution and the genetics of populations, vol. 4, variability within and among natural populations. Chicago, IL, USA: University of Chicago Press; 1979.
- [18] Stone AC, Griffiths R, Zegura S, Hammer M. High levels of Y chromosome nucleotide diversity in the genus *Pan*. *Proc Natl Acad Sci USA* 2002;99:43–8.
- [19] Goodrum J. The race FAQ. <http://www.goodrumj.com/RFAQHTML.html>; 2002 [accessed 24.06.09].
- [20] Wise C, Sraml M, Rubinsztein D, Easteal S. Comparative nuclear and mitochondrial genome diversity in humans and chimpanzees. *Mol Biol Evol* 1997;14:707–16.
- [21] Jorde L, Rogers A, Bamshad M, et al. Microsatellite diversity and the demographic history of modern humans. *Proc Natl Acad Sci USA* 1997;94:3100–3.
- [22] Bowcock AM, Ruiz-Linares A, Tomfohrde J, Minch E, Kidd JR, Cavalli-Sforza LL. High resolution of human evolutionary trees with polymorphic microsatellites. *Nature* 1994;368:455–7.
- [23] Reinartz GE, Karron JD, Phillips RB, Weber JL. Patterns of microsatellite polymorphism in the range-restricted bonobo (*Pan paniscus*): considerations for interspecific comparison with chimpanzees (*P. troglodytes*). *Mol Ecol* 2000;9:315–28.
- [24] Van Hooft WF, Groen AF, Prins HHT. Microsatellite analysis of genetic diversity in African buffalo (*Syncerus caffer*) populations throughout Africa. *Mol Ecol* 2000;9:2017–25.
- [25] Uphyrkina O, Johnson WE, Quigley H, et al. Phylogenetics, genome diversity and origin of modern leopard, *Panthera pardus*. *Mol Ecol* 2001;10:2617–33.
- [26] Eizirik E, Kim J, Menotti-Raymond M, Crawshaw Jr PG, O'Brien SJ, Johnson WE. Phylogeography, population history and conservation genetics of jaguars (*Panthera onca*, Mammalia, Felidae). *Mol Ecol* 2001;10:65–79.
- [27] Culver M, Johnson WE, Pecon-Slattery J, O'Brien SJ. Genomic ancestry of the American puma (*Puma concolor*). *J Hered* 2000;91:186–97.
- [28] Schwartz MK, Mills LS, McKelvey KS, Ruggiero LF, Allendorf FW. DNA reveals high dispersal synchronizing the population dynamics of Canada lynx. *Nature* 2002;415:520–2.
- [29] Paetkau D, Amstrup SC, Born EW, et al. Genetic structure of the world's polar bear populations. *Mol Ecol* 1999;8:1571–84.
- [30] Paetkau D, Waits L, Clarkson P, et al. Variation in genetic diversity across the range of North American brown bears. *Con Biol* 1998;12:418–29.
- [31] Waits L, Taberlet P, Swenson JE, Sandegren F, Franzén R. Nuclear DNA microsatellite analysis of genetic diversity and gene flow in the Scandinavian brown bear (*Ursus arctos*). *Mol Ecol* 2000;9:421–31.
- [32] Garcia-Moreno J, Matocq M, Roy M, Geffen E, Wayne RK. Relationships and genetic purity of the endangered Mexican wolf based on analysis of microsatellite loci. *Con Biol* 1996;10:376–89.
- [33] Girman DJ, Vil C, Geffen E, et al. Patterns of population subdivision, gene flow and genetic variability in the African wild dog (*Lycaon pictus*). *Mol Ecol* 2001;10:1703–23.
- [34] Wilton AN, Steward DJ, Zafiris K. Microsatellite variation in the Australian dingo. *J Hered* 1999;90:108–11.
- [35] Kyle CJ, Strobeck C. Genetic structure of North American wolverine (*Gulo gulo*) populations. *Mol Ecol* 2001;10:337–47.
- [36] Walker CW, Vil C, Landa A, Lindén M, Ellegren H. Genetic variation and population structure in Scandinavian wolverine (*Gulo gulo*) populations. *Mol Ecol* 2001;10:53–63.
- [37] Polziehn RO, Hamr J, Mallory FF, Strobeck C. Microsatellite analysis of North American wapiti (*Cervus elaphus*) populations. *Mol Ecol* 2000;9:1561–76.
- [38] Forbes SH, Hogg JT, Buchanan F, Crawford A, Allendorf F. Microsatellite evolution in congeneric mammals: domestic and bighorn sheep. *Mol Biol Evol* 1995;12:1106–13.
- [39] Barbujani G, Magagni A, Minch E, Cavalli-Sforza LL. An apportionment of human DNA diversity. *Proc Natl Acad Sci USA* 1997;94:4516–9.
- [40] Hartl D, Clark AG. Principles of population genetics. Sunderland, MA, USA: Sinauer Associates; 1998.
- [41] Coon CS. The origins of races. New York, NY, USA: Alfred A. Knopf; 1962.
- [42] Nei M, Roychoudhury A. Evolutionary relationships of human populations on a global scale. *Mol Biol Evol* 1993;10:927–43.
- [43] Cavalli-Sforza LL. Genes, peoples and languages. San Francisco, CA, USA: North Point Press; 1991.
- [44] Cavalli-Sforza LL, Menozzi P, Piazza A. The history and geography of human genes. Princeton, NJ, USA: Princeton University Press; 1994.
- [45] Andreason RO. The cladistic race concept: a defence. *Biol Phil* 2004;19:425–42.
- [46] Andreason RO. A new perspective on the race debate. *Br J Philos Sci* 1998;49:199–225.
- [47] Cartwright SA. Natural history of the prognathous species of man. New York, NY, USA: New York Day; 1857.
- [48] Eldridge N, Cracraft J. Phylogenetic analysis and the evolutionary process: method and theory in comparative biology. New York, NY, USA: Columbia University Press; 1980.
- [49] Mishler BD, Theriot EC. The phylogenetic species concept (sensu Mishler and Theriot): monophyly, apomorphy, and phylogenetic species concepts (three chapters). In: Wheeler Q, Meier R, editors. Species concepts and phylogenetic theory: a debate. New York, NY, USA: Columbia University Press; 2000.
- [50] Platnick NI, Wheeler QD. A defense of the phylogenetic species concept (sensu Wheeler and Platnick). In: Wheeler Q, Meier R, editors. Species concepts and phylogenetic theory: a debate. New York, NY, USA: Columbia University Press; 2000.
- [51] Rushton JP, Russell RJH, Wells PA. Genetic similarity theory: beyond kin selection. *Behav Genet* 1984;14:179–93.
- [52] Salter FK. On genetic interests: family, ethny, and humanity in an age of mass migration. Frankfurt, Germany: Peter Lang; 2003.
- [53] Salter FK. On genetic interests: family, ethnicity, and humanity in an age of mass migration. Edison, NJ, USA: Transaction Publishers; 2005.
- [54] Fuerle RD. Erectus walks amongst us. New York, NY, USA: Spooner Press; 2008.
- [55] Caramelli D, Lalueza-Fox C, Vernesi C, et al. Evidence for a genetic discontinuity between Neandertals and 24,000-year-old anatomically modern Europeans. *Proc Natl Acad Sci USA* 2003;100:6593–7.
- [56] Curnoe D, Thorne A. Number of ancestral human species: A molecular perspective. *HOMO* 2003;53:201–24.
- [57] Gutiérrez G, Sánchez D, Marín A. A reanalysis of the ancient mitochondrial DNA sequences recovered from Neandertal bones. *Mol Biol Evol* 2002;19:1359–66.
- [58] Jensen-Seaman M. Western and eastern gorillas: estimates of the genetic distance. *Gorilla J* 2000;20:21–3.
- [59] Guillén A, Barrett GM, Takenaka O. Genetic diversity among African great apes based on mitochondrial DNA sequences. *Biodivers Conserv* 2005;14:2221–33.
- [60] Thalmann O, Fischer A, Lankester F, Pääbo S, Vigilant L. The complex evolutionary history of gorillas: insights from genomic data. *Mol Biol Evol* 2006;24:146–58.
- [61] Becquet C, Patterson N, Stone AC, Przeworski M, Reich D. Genetic structure of chimpanzee populations. *PLoS Genet* 2007;3:e66. doi: 10.1371/journal.pgen.0030066.
- [62] Whitlock M, McCauley D. Indirect measure of gene flow and migration: F_{ST} [does not equal] $1/(4Nm + 1)$. *Heredity* 1999;82:117–25.
- [63] Charlton BG. The James Watson affair. *Med Hypotheses* 2008;70:1077–80.
- [64] Omolja A, Mitsnefes M, Talley L, Benfield M, Neu A. Racial differences in graft survival: a report from the North American pediatric renal trials and collaborative studies (NAPRTCS). *Clin J Am Soc Nephrol* 2007;2:254–8.
- [65] Spierings E, Hendriks M, Absi L, et al. Phenotype frequencies of autosomal minor histocompatibility antigens display significant differences among populations. *PLoS Genet* 2007;3:e103. doi: 10.1371/journal.pgen.0030103.
- [66] Holden C. Race and medicine. *Science* 2003;302:594–6.
- [67] Brewer RM. Thinking critically about race and genetics. *J Law Med Ethics* 2006;34:513–9.

- [68] Duster T. Lessons from history: why race and ethnicity have played a major role in biomedical research. *J Law Med Ethics* 2000;34:487–96.
- [69] Lillquist E, Sullivan CA. Legal regulation of the use of race in medical research. *J Law Med Ethics* 2006;34:535–51.
- [70] Roberts DE. Legal constraints on the use of race in biomedical research: toward a social justice framework. *J Law Med Ethics* 2006;34:526–34.