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Lineage Population: A Concept Needed by an Observer of Nature?

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The genealogy-based classificatory programs of Kant and Darwin are briefly discussed for context. It is detailed how in biology there is no unambiguous term to reference infraspecific-level descent-based divisions. The term *lineage population* is introduced and defined for analytic purposes as one of a set of inter-fertile divisions of organisms into which members are arranged by propinquity of descent. It is argued that the lineage population concept avoids the ambiguities associated with related biological and anthropological concepts and polysemes such as *population*, *ethnicity*, and *race*. Other terms and concepts, such as *form*, *cline*, *cluster*, *geographic population*, *breeding population*, *genetic population*, *breed*, *species*, *subspecies*, *ancestry*, *geographic ancestry*, *biogeographic ancestry*, *ancestral population*, *ancestry population*, *natural division*, and *population lineage*, are discussed in relation to this concept. It is concluded that the lineage population concept is a useful analytic tool which describes, in line with the Kantian/Darwinian perspective, an interesting class of biological variation.

Key Words: Systematics, Kant, Darwin, Lineage population, Population, Ethnicity, Race, Population lineage

Descent was first proposed as an organizing principle for natural history during the 18th century,¹ but only during the 19th century, with the acceptance of

¹ Natural history (lt. *historia naturalis*), in the 18th and 19th century sense, referred to the study of nature and natural objects. The focus encompassed, among other domains, zoology, botany, and biological anthropology. While the applied biological sciences, such as animal husbandry and agriculture, were frequently discussed and made reference to

evolutionary theory, did it become widely adopted. Despite general acceptance of phyletic-based² classification and analysis, nomenclature has remained confused and ambiguous, especially on the infraspecific level. While the term *race* was previously used to denote descent-based groupings either on the specific, subspecific, or infrasubspecific level, a number of biologists and anthropologists have come to feel that the word is problematic and that more precise terms are called for (for example: Wagner et al., 2016). Unfortunately, alternative terms and concepts are presently either ambiguous or nonspecific, respectively. Heeding the call for precision, the neutral term, *lineage population*, is introduced and defined to correspond with Darwinian infraspecific and specific “communities of descent.” This concept is discussed in relation to other biological and anthropological terms and concepts.

1. Systematics and the Kantian/Darwinian principle

Over two hundred years ago, Immanuel Kant (1777, 1788) argued that the guiding principle for natural history, insofar as one wished to understand patterns of variation, should be genealogical relationship. He contrasted *scholastic* with *natural* divisions and stated that “a natural division is based upon identifying lines of descent that classify animals according to reproductive relationship” (1777). The Kantian principle for natural history was summarized in 1796 by Christoph Girtanner, who wrote that a new Kantian “system of classification for the animal kingdom into classes, orders, species, races, variations, and varieties [developed] according to relationships of generation, must be taken up.” The principle was likewise critiqued by naturalist Georg Forster who argued, on the basis of Linnaean systematics, that it was impossible to trace infraspecific lines of descent. Forster (1786) notes: “[The situation] must be different in natural history, if, in this [field] we are, as Kant claims, concerned only with generative origination and descent. Natural history in this sense might, however, possibly be only a science for gods and not for human beings.” Kant’s descent-based principle for natural history led directly to his conception of race, which was seen as necessary “for an observer of nature... from the viewpoint of natural history” (1788). *Races* were one of the manifold of possibilities which could potentially characterize biological variation understood from a genealogical perspective; conceptually, they were “progenies *classificae*,” lines of descent or deviate forms that “are still

in order to explain natural historian theories and concepts, these fields were generally not considered to be part of natural history proper.

² This is a disputed term. Meant here is Mayr’s Haeckelian sense of “pertaining to lines of descent.” See: Mayr & Bock (2002).

so distinct and persistent that they justify a class distinction” (1788); in practice, they were infraspecific groups of organisms which exhibited hereditary characters with a uniformity sufficient to allow for a descent-based classification.³

Kant is of primary interest because he was the first to clearly recognize and to forcefully articulate the view that a “natural” system for natural history would be a descent-based one (Doron 2012). His conceptualization had a lasting impact because both his perspective on natural history and his race concept were adopted by others, such as the influential naturalist Johann Blumenbach (Lenoir 1980). Linnaean systematics having been overturned,⁴ the descent-based organizing principle is now foundational to biology, including the subfields of taxonomy, conservation biology, evolutionary biology, and population genetics. As such, groups of organisms – on the infraspecific, specific, and supraspecific level – are conceptually related to one another in terms of genealogical affinity since propinquity of descent, “the only known cause of the similarity of organic beings, is the bond, hidden as it is by various degrees of modification” (Darwin 1859, 413-414). The rationale for this organizing principle was articulated by economist and philosopher William Jevons in *Principles of Science* (1874, 680-719):

It is true that in the biological sciences there would be one arrangement of plants or animals which would be conspicuously instructive, and in a certain sense natural, if it could be attained, and it is that after which naturalists have been in reality striving for nearly two centuries, namely, that *arrangement which would display the genealogical descent of every form from the original life germ*. Those morphological resemblances upon which the classification of living beings is almost always based are inherited resemblances, and it is

³ Conceptually, for Kant, *race* simultaneously described the lineage diagnosing characters which were transmitted along lines of descent; the lines of descent themselves; and the classes of organisms which were delineated by these characters, such as skin color (Kant, 1785) and possibly skeletal form (Kant, 1788). In practice, though, races inevitably referred to classes of organisms.

⁴ Linnaeus' views evolved but his early ones were most influential. Accordingly, the members of Linnaean species, representing originally distinct lineages, were understood as being united in descent; and both supraspecific and infraspecific groupings of organisms (Linnaean classes, orders, and varieties) were only resemblance-based. Linnaeus conducted hybridization experiments over his career and discovered that certain of his species and other higher order groupings were interfertile, which led him to conclude that many of what he originally called species were not originally distinct lineages, which were expected to be intersterile.

evident that descendants will usually resemble their parents and each other in a great many points.... There is no reason to suppose that the same kind of natural classification which is best in biology will apply also in mineralogy, in chemistry, or in astronomy.

While Kant's views were indirectly influential,⁵ it was Charles Darwin who established the primacy of descent for classifying organisms and understanding the relationships amongst them. Darwin's position was quite similar to that later expressed by Jevons (1874). For Darwin, a descent-based classification was seen as both a natural one and one in which systematics⁶ should be grounded, because commonality in descent explained most organismic similarity and because arranging by descent had the effect of grouping organisms by overall phenetic similarity, which is what early systematicists, from Linnaeus on,⁷ strove for. In this descent-based system, *race* found a place in natural history as a description of specific and infraspecific communities of descent. Commenting to Thomas Huxley in 1867 on a *natural system* and a classification of human races, Darwin noted:

I knew, of course, of the Cuvierian view of Classification, but I think that most naturalists look for something further, & search for "the natural system", – "for the plan on which the Creator has worked" etc. etc. – It is this further element which I believe to be simply genealogical....

Grant all races of man descended from one race; grant that all structure [i.e., physical features] of each race of man were perfectly known – grant that a perfect table of descent of each race was perfectly known – grant all this, &

⁵ Kant's definition of *race*, for example, was cited in Blumenbach's widely read *A Manual of the Elements of Natural History* (1825, 15-16).

⁶ Here, Mayr and Ashlock's (1991, 431) broad conception of systematics is adopted: "The science dealing with the diversity of organisms." Taxonomy, the "theory and practice of classifying organisms," is nested within this. By this term usage, a "breed" is a systematic classification or unit but not a taxonomic category/rank.

⁷ Bowler (1989, 65) succinctly notes: "It must be supposed that in the Creator's plan every relationship has a meaning; thus a truly natural system of classification will have to take into account all the characteristics of every species. Linnaeus believed that such a natural system was the goal of his work, although at the beginning of his career, he was overwhelmed by the immense amount of information that would have to be processed in order to set up a natural system. As a preliminary set, he decided to establish an 'artificial system' that would classify according to resemblance in a *single* characteristic."

then do you not think that most would prefer as the best classification, a genealogical one, even if it did occasionally put one race not quite so near to another, as it would have stood, if allocated by structure alone. Generally, we may safely presume, that the resemblance of races & their pedigrees would go together. (Darwin, 1903, letter 204)

1.1. *Semiotic ambiguity of race, past and present*

Prior to the 18th century, the French term *race*, which in ordinary usage primarily meant lineage⁸, was not infrequently used to refer to humanity or to human divisions understood in terms of lineage. Thus, for example, historian Sir Paul Rycaut (1668) could comprehensibly discuss groups of the Ottoman Empire in a decidedly genealogical fashion⁹, and many of the groups described as *races* by Rycaut, such as Tartars or Turks, correspond with *races* discussed by 18th century natural historians, such as Buffon (1777). Yet, prior to the 18th century, such *races* found no place in a coherent biological systematics for the simple reasons that a modern concept of biological species – which *race*, as a natural scientific concept, has always been defined in relation to – was missing and that humans were not treated as part of natural history. For the former one had to wait for John Ray (Wilkins 2009, 65-67) and for the latter Carl Linnaeus (Smith 2015, 136-138). Contrary to what is sometimes said or suggested (for example: Lieberman, 1968), Linnaeus himself did not introduce *race* – either the term or a unique concept which might reasonably be called this – into natural history. On the contrary, the systematic categories which he popularized, those of *variety* and *species*, left no epistemic space in natural history for *race* (at least one not redundant with *species*) (Doron 2012; see footnote 11). It was both because it

⁸ For example, in *A Dictionarie of the French and English Tongues* compiled by Randle Cotgrave in 1611, *race* is defined as: “a linnage, familie, kindred, house, blood; litter, brood; sort, kind...”; in Pierre Richelet’s (1757) *Nouveau dictionnaire françois*, *race* is defined as: “lignee. Extraction. Desendans. Famille. Sorte de gens. Espece”; in Noël and Chapsal’s (1832) *Nouveau dictionnaire de la langue française*, *race* is defined as “(radix, gen, icis) extraction, origine; lignee; tousceux qui viennent de meme famille.”

⁹ Rycaut (1668) notes, for example, that: “They that are of this Race never dare vaunt of their Pedigree, it is a contumaciousness and almost Treason to name it; nor have I learned that there is any Family amongst the Turks of this Line, of any account or esteem, but one alone, who is called Ibrahim Hun Ogleri, or the Off-spring of Sultan Ibrahim, their Father being a Son of the Grand Signior’s Sister, and married to a Sultana (and are said to be of the Race of the Tartars) so that proceeding by the Women’s side only, the less notice is taken of their Blood...”

became obvious that there was something to explain – the constancy of so-called constant varieties – and it was often unclear if these propagating forms represented infraspecific as opposed to specific lineages that the terminology of *race* was adopted.

Darwin (1871) and others recognized that the term *race* lent itself to confusion as, in the context of natural history, it could refer to species, subspecies, hereditary varieties, and domestic breeds – all understood as lineages and/or forms which propagate themselves across generations to form lineages. While the term's pedigree seems to have been well appreciated, there was, from the start, disagreement regarding how restrictively it should be employed. Thus contra Kant (1777), who delimited the term *race* to describe infraspecific divisions,¹⁰ Forster (1786) rejected the Kantian principle in favor of Linnaean systematics with its species versus inconstant variety distinction,¹¹ a distinction which made no room for Kant's concept of race. Forster argued that the term *race* should be used in an undetermined way to describe lineages, whether they constituted, as he saw the alternatives, Linnaean species or Linnaean varieties. Understood in the latter sense, races were “defined by changeable, accidental characteristic features” such that “one variety can change into another” and had no real place in natural history (1786). Forster writes:

¹⁰ Though, in his *Lectures on Anthropology*, Kant frequently refers to the “human race,” meaning the human species; so across works he is not consistent on the matter. But, for an exclusively infraspecific definition, see also Duchesne (1766, 18-26) and, by way of Kant, Blumenbach (1825, 15-16).

¹¹ Müller-Wille (2007) notes: “At the core of Linnaeus's reform stood his distinction between species and variety which was thoroughly based on his theory of generation. In distinguishing between species, Linnaeus advised his fellow naturalists, one should rely exclusively on “constant” characters – that is, not on characters that varied with external conditions like climate or nutrition, but on characters that reproduced in offspring under various external circumstances.” Briefly, in Linnaean systematics, species were *defined* in terms of separate origins (but see footnote 3) and *diagnosed* by their ability to reproduce their form across generations. Varieties, in contrast, were *defined* as environmentally induced deviations from the species form and they were *diagnosed* by their inconstancy across different environments. It was soon realized that some peculiarities within what seemed to be the same species line of descent were constant (across environments), which led to the oxymoronic term *constant varieties* and to lumpers-splitter debates as to whether various groups, given the relative constancy of their forms, were *varieties* or *species*.

I have deliberately made use of the word *variety* in the previous discussion, but [I have] at the same time given it to be understood that I consider it synonymous with [the word] *race*....

We have borrowed [the term] from the French; it seems very closely related to [the words] *racine* and *radix* and signifies descent in general, though in an indeterminate way. For one talks in French of the race of Caesar [in] the same [way] as of the races of horses and dogs, irrespective of the first origin, but, nevertheless, as it seems, always with tacit subordination under the concept of a species.... [The word] should mean nothing more than a mass of men whose common formation is distinctive and sufficiently at variance with their neighbors [such that they] could not be *immediately* derived from them. [They are] a lineage whose derivation is unknown, and consequently, one which we cannot easily count under one of the commonly accepted human varieties because we lack knowledge of the intermediary link. Thus, the Papuans and the other black inhabitants of the islands of the South Sea related to them are called a different *race* [distinguishable] from the light brown people of Malaysian descent that can be found in the same region. [This, however, is only to say] that [they are] *a people of peculiar character and unknown descent*.

Forster was hardly the only one who had something to say about term usage. French naturalist Jean Baptiste Bory de Saint-Vincent and Marcellin (1827, 63) criticized monogenists for trying to evade the conclusion that different human groups were different species “by referring to ‘races,’ probably not remembering that the word *race*, synonymous with lineage, is most usually used in speaking of domestic animals...” For Bory de Saint-Vincent, as for Forster, *race* did not have a real, non-redundant place in (Linnaean) systematics – thus groups were either species or Linnaean varieties.¹² Approaching the matter from the other side of the debate, natural historian Armand de Quatrefages (1861, 311) excoriated the American polygenist school for “assimilating” the term *race* and for failing to draw

¹² Bory de Saint Vincent (1827, 70) notes: “It would be necessary to prove that whites and negroes differ due to climate in which they live, that the lineage of negroes and whites have changed, without crossbreeding from white to black, or from black to white, after having been carried from south to north or from north to south.” Here, he is employing the species/inconstant variety dichotomy to defend the claim of the plurality of human species.

the proper distinctions between the *race* and *species* concepts. De Quatrefages writes:

Let us first notice in MM. Nott and Gliddon the complete assimilation of the two words *race* and *species*. – In Europe, all botanists, all zoologists, from Linnaeus to de Candolle, from Buffon to Cuvier, and Geoffroy Saint-Hilaire, have employed them to designate very different things. If some have designated *race* by the expression *hereditary variety*, this difference in words does not in any way affect ideas.

The distinction which exists all facts considered is always translated into language. Yet it is this distinction that the American school seems to forget entirely here. For her, there are no more *races* or *varieties* in nature; there are only *species*.

De Quatrefages' historiography is problematic as, for example, Buffon and Cuvier called both specific and infraspecific lineages *races*, but that is another matter. What is relevant is that *race* concepts were disputed and that the term was employed differently by different researchers, situations which led to confusion and ambiguity. At issue was not only whether *race*, properly understood, referred exclusively to infraspecific or inclusively to both infraspecific and specific lineages. As Bory de Saint-Vincent's comment suggests (cited above), some thought that the proper denomination of the term was to refer to domestic breeds. Thus, Deniker (1906, 4-8) questioned whether one can properly speak of human *races* in a technical zoological sense, since according to him, the term typically describes "domestic animals living under artificial conditions." He opted to use *race* in "a very broad sense, different from that given to it in zoology and zootechnics." Paul Broca (1864) noted another concern: that certain polygenists were using the term in a "general and misleading sense" to refer to collections of (Linnaean) *species*. Broca criticized these researchers on account of their uncritical and self-defeating adoption of the "ambiguous term *race*" (1864, 14) to refer to, in addition to *species* and infraspecific lineages, polyphyletic groups. He noted:

[These other polygenists] continue also very often to use the term *race* to designate the ensemble of all individuals of each group, adopting this by a sort of transaction of language of those whose system they reject; and thus they speak of the white or Caucasian *race*... as if, for instance, the brown Celts and the fair-haired Germans had descended from the same primitive stock. This contradiction has given a handle to monogenists; for if climate and mode of life can cause a German to become a Celt, there is no reason why,

under certain influences, a Celt might not become a Berber, a Berber a Foulah, a Foulah a Negro, and a Negro an Australian.

Of course, when discussing the “human species” or the “human race” polygenists (for example: Virey (1837, 102-104) would also have employed terms in misleading senses, since humanity, so conceptualized, would constitute a polyphyletic group equivalent to a Linnaean supraspecific division. With the acceptance of evolutionary theory, the classic ontological distinction between specific, infraspecific, and supraspecific classes vanished and with it some of these semantic concerns. It was no longer that, as Linnaeus put it, “Nature makes species and genus, culture makes varieties, art and nature makes classes and orders” (Fundamenta Botanica 1737, qtd. in Stamos 2005) and so one could treat infraspecific races, species, and closely allied species as roughly the same type of thing. Before the acceptance of evolution, the term *race* allowed one to write ambiguously of population lineages without committing oneself to a position as to the origin of these. After, one could do the same, but without eliding an important ontological distinction. This generic usage, while having utility, as noted by Gray (1879, 320-321),¹³ has contributed nontrivially to the cloud of confusion surrounding the term. For example, it led William Boyd (1950, 186-187), hardly an opponent of race concepts, to conclude, based on his mid-20th century etymological analysis of the word *race*, that the “implication of the separate origins for different races came inevitably....” The sense of *race* Boyd is speaking of, though, is none other than Forster’s *species*, and Forster and other polygenists,¹⁴ as suggested above, recognized that the *race* notion undercut the force of their argument for separate origins. It was part of, as Paul Broca (1864, 10) put it, the “language of those whose system” the polygenists rejected. That is, contra Boyd, the generic notion of *race* was employed by monogenists in their explanation of how groups could transmit their character differences across generations – could

¹³ Gray (1879, 320-321) notes: “Wherefore, since we hardly need the term race in the restricted sense of seed-propagating variety, it is sometimes convenient to use it in the manner proposed by Bentham ... as the common designation of any group or collection of individuals whose characters are continued through successive generations, whether permanent variety, subspecies, species, or group consisting of very similar species, the term not implying any decision of this question. If this use of the term prevails, *Subspecies*, will probably take its place as the designation of the highest grade of variety.”

¹⁴ The term polygenist is used in the original sense of those who argued that different human groups represented separate creations or autochthonic lineages and thus separate species.

be forms which propagated themselves across generations – without being separate Linnaean species.¹⁵

Between the middle of the 18th century to the second half of the 19th century, it was frequently debated whether human and other lineage-based divisions were *races qua* Linnaean species or *races qua* varieties.¹⁶ These debates were substantive in that interlocutors agreed on a common, non-conventional definition of species – originally distinct lineages – but disagreed when it came to what constituted evidence for separate origins. As Wallace (1864) points out, monogenists argued that continuance in variation, a lack of homogeneity, interfertility between groups, and a difficulty in delineating groups evidenced that the various races were constant varieties (for example: Prichard 1836). Polygenists, on the other hand, rejected these diagnostic criteria and emphasized that popularized by Linnaeus.¹⁷ During the 20th century and continuing into the

¹⁵ See, for example, Pierre Louis Maupertuis's account of inherited differences between human races in *Venus physique* (1745), an account which was picked up by the widely influential Comte de Buffon. See, also, Duchesne's (1766, 18-19) discussion of why the concept of race was needed so to prevent one from being forced to rank human (constant) varieties as separate species: "It often happens that instead of the word Race, Species is employed; which obliges species to be given the name of genera; thus, instead of saying that in the human species, there are several races, that of white men, that of black men, etc.; whites and blacks are regarded as distinct species, which make up the human race. I confess that this way of expressing oneself would be more in accordance with the etymologies which I have just related... but this usage is actually not that of scientists..."

¹⁶ In botany and zoology there were "lumper-splitter" or "variety-species" debates parallel to the anthropological monogenist-polygenist ones (see: Stamos 2007), though the term *race* was less commonly used in these discussions to denote lineages in the most general sense.

¹⁷ Often missed in discussions is that the polygenist understanding of species was very minimalistic; species were only expected to exhibit at least one hereditary character difference (Broca & Blake 1864; Forster 1786; see also Wallace's (1864) characterization of the position). Thus, for example, Forster took the constancy of pigmentation differences between Europeans and Black Africans as evidence that the races were separate Linnaean *species*, as opposed to separate Linnaean *varieties*. He notes: "Is the Negro a *variety* or a *species* in the human genus? If [the ruling in this matter] depends upon proving the descent of all varieties from an original, common parental couple, which cannot be demonstrated without indisputable historical evidence, there will be no definite solution... If, on the other hand, we are satisfied by the Linnaean ruling, [that] a variety differs from a species simply through the inconstancy of its characteristic features, then a little provisional investigation is still required [to find out] to what extent this definition fits

21st, anthropologists began debating whether the human divisions previously called *races* really qualified as *races*.¹⁸

Whereas the 18th to early 19th century species/variety debates were substantive, these were and are mostly semantic, turning on the users' specification of the term race. During this time, many proponents of the "no-races" position narrowly constructed the meaning of *race* – so that the word implied markedly discontinuous populations, separate homogeneous populations, populations between which there were extensive genetic differences, divisions between which there had been extensive reproductive barriers, etc.¹⁹ – to mean something closer to the polygenists' Linnaean species and, on the basis of these understandings, deemed that race, the construct, had either no biological validity or no applicability to humanity. Others, deeming that *race* implied populations between which there were phyletic discontinuities²⁰ significant enough to enable

the various human lines of descent." Virey (1837, 19-35) makes roughly the same argument: "In whatever light we consider Negroes, we cannot deny that they present characteristics of a race distinct from the white. This truth, grounded upon incontestable facts of anatomy, is universally acknowledged. Now, in natural history, that which distinguishes a *species* from a *race*, is the permanency of the characteristic features, notwithstanding contrary influences of climate, food, or other external agents: whereas, races are but varied modifications of a sole and primordial *species*... [W]hy do [negroes] not remain white in cold countries, and when kept from the light? If the blackness of their skin was produced by a cause entirely occasional and external why should it be hereditary in all countries, and the same in all generations?...Everything serves to prove that negroes form, not only a *race*, but undoubtable a *distinct* species, from the beginning of the world."

¹⁸ See Lieberman (1968), Lieberman and Reynolds (1978), and Littlefield et al. (1982) for an outline of the history of the human "race-exists" and "no-race" positions debate.

¹⁹ See Lieberman, Kirk and Corcoran's (2000) Table 2. The authors note: "Lieberman and Kirk's survey of 1999 asked respondents about their support or rejection of biological race and found that among those who rejected the race concept 79 percent supported analyzing variation in terms of clines rather than races, 78 percent rejected the idea of homogeneous populations, 80 percent supported more variation within so called races than among them and, for 88 percent, gene flow invalidated labeling distinct races (Table 2)." It is not made clear why *races* came to be seen as entailing these characteristics. Based on the characterization of the "19th century idea of race" which the authors seem to accept, poor historiography seems to have played a part.

²⁰ Littlefield et al. (1982), for example, note: "More recently, the race concept has been attacked as invalid because populations of humans separated by significant reproductive

the objective partitioning of the species, concluded that the human divisions previously called races did not count as bona fide natural historian *races*.²¹

In defense of this position it was claimed that human races do not exist because human groups “grade one into another” (Brace 1964) and because “[b]oundaries between what have been called 'races' are completely arbitrary, depending primarily upon the wishes of the classifier” (Brace 1964; Lieberman 1968). On this point, Lieberman and Reynolds (1978) tell us that “[t]he issue is not whether there is factual proof of hereditary variations” but whether character variation is distributed “in such a discordant pattern that identifiable boundaries cannot be established...” Yet, originally, the central issue was, in fact, the nature and status of hereditary variation, that is, of seed-propagating forms, and not what would now be called population structure. Regarding the latter topic, as noted above, gradation, especially in the human genus, was well recognized and was the basis for one common argument for why divisions were races *in the infraspecific sense*, that is, were hereditary varieties – a point which Brace (1964) and Lieberman (1968) tacitly acknowledge with their remarkable reference to none other than Blumenbach as the originator of this argument.²² At the same time, theoretical paradigms changed, and proponents of the position that (human) races exist correspondingly updated their concepts.²³ The result of the conceptual

barriers and/or exhibiting concordant combinations of variable physical traits cannot be shown to exist.”

²¹ Some, such as Ashley Montagu (1942), granted that, of course, human races exist in a zoological and genetic sense, but argued against supposed popular conceptions, such as, for example, race as the “prime determiner of all the important traits of body and soul, of character and personality, of human beings and nations” (pp. 9).

²² Similarly, Smith (2015, 256) notes: “For a reifier of race, we see here, Blumenbach certainly cedes quite a bit to what we today would call the constructionist camp.” The difference is that Brace (1964) and Lieberman (1968) – along with many contemporaneous anthropologists and philosophers of biology – see the “constructivism,” well-recognized by early “reifiers of race,” involved in infraspecific racial classifications, especially human ones, as an argument against these classifications.

²³ Some, for example Hochman (2013), have argued that proponents of the position that human races exist have watered down the concept of race; however, it’s hard to reconcile this position with typical 18th and 19th century usages, in which the term was broadly employed to refer to both species and constant varieties and as the latter was conceptualized in a very “weak naturalistic” sense; for example, Gray (1879, 320) defines race, in the narrow technical sense, as “a variety which is perpetuated with considerable certainty by sexual propagation.”

revisions is that there are multiple disputed meanings of the term (Lieberman et al. 2004).

Unfortunately, contemporaneous biological definitions, often being less than transparent, have done little to help resolve the semiotic confusion. While contemporaneous dictionaries of biology, genetics, and zoology frequently define the term (for example, Martin & Hine 2008; Allaby 2013²⁴), the definitions are often opaque and not obviously tethered to the historic sense of lineage. Compare these definitions with Gould (1894) and Beeton (1871),²⁵ where the understanding of lineage, stock, or propagating form is more obvious.

By these definitions, human and non-human races obviously exist – in the way that other groupings such as morphs, forms, and demes do (i.e., the concepts have applicability) – but it is not clear to what extent the term refers to a concept or conceptual network reasonably similar to what it once generally did. For example, in the 8th edition of *A Dictionary of Genetics*, King, Mulligan, and Stansfield (2013) define *subspecies* and *race* in the following manner:

subspecies 1. a taxonomically recognized subdivision of a species. 2. geographically and/or ecologically defined subdivisions of a species with distinctive characteristics. See race. (p. 456)

race a phenotypically and/or geographically distinctive subspecific group, composed of individuals inhabiting a defined geographical and/or ecological region, and possessing characteristic phenotypic gene frequencies that distinguish it from other such extension groups. *Homo sapiens* can be subdivided into five races on the basis of geographic origin. (p. 391)

²⁴ Martin and Hine (2008, 500) define race as: “(in biology) A category used in the classification of organisms that consists of a group of individuals within a species that are geographically, ecologically, physiologically, or chromosomally distinct from other members of the species... (in anthropology) A distinct human type possessing several characteristics that are genetically inherited.” Allaby (2013, 478) defines race as: “An interbreeding group of individuals all of whom are genetically distinct from the members of other such groups of the same species. Usually these groups are geographically isolated from one another, so there are barriers to gene flow.”

²⁵ Gould (1894, 1231) defines race as: “In biology, a genealogic, ethnic, or tribal stock; a breed or variety of plants or animals made permanent by constant transmission of its characters through the offspring....” Beeton (1871, 239) defines race as: “In Bot., those permanent varieties of species which can be propagated by seed.”

King, Mulligan, and Stansfield's *subspecies* are formally recognized *races*; they are taxa assigned to the taxonomic category or rank immediately below that of species.²⁶ But what their *races* are and how they are precisely delineated is unclear. According to their definition, *races* are "populations"²⁷ which differ in hereditary phenotypic characters. When it comes to humans, *races* are said to be divisions based on "geographic origin," not contemporaneous geographic location; thus *races* – at least human ones – are not strictly geographic populations. Imaginably, if pressed on the matter, the authors would make the same types of clarifications that O'Brien and Mayr (1991) and Mayr (2002) have.

According to O'Brien and Mayr (1991), who attempt to clarify the meaning of *subspecies*, the members of a subspecies "share a unique geographical range or habitat, a group of phylogenetically concordant phenotypic characters, and a unique natural history relative to other subdivisions of the species." The sharing of phyletic-based characters and a unique natural history implies genealogical affinity between members – and thus that the concept aligns with that of *natural divisions* in the Darwinian sense and finds a meaningful place in a phyletic-based taxonomy. Regarding human races, Ernst Mayr (2002) tells us:

A human race consists of the descendants of a once-isolated geographic population primarily adapted for the environmental conditions of their original home country. But, as is illustrated by the success of Europeans and Africans and Asians in all parts of the world, any race is capable of living anywhere.

Accordingly to Mayr (2002), the human species was recently comprised of populations, ones relatively geographically isolated for a number of generations, which "agree in most characteristics with the geographic races of animals." Presently, he tells us, human races are the sum of the – presumably, relatively purebred – descendants of these isolated populations. Since members of human races can live anywhere, for Mayr, propinquity of descent seems to stand as the classifying criterion for *race* in the most general sense. Perhaps King, Mulligan,

²⁶ A taxon (pl. taxa) is a particular group of organisms that is given a formal name (e.g., *Hippopotamus amphibius*) and assigned to a definite taxonomic category (e.g., species). A taxonomic category is a rank in a hierarchal ordering of life.

²⁷ A *population* is defined as "a local (geographically defined) group of conspecific organisms sharing a common gene pool; also called a *deme*" (p. 370). A *deme* is defined as "a geographically localized population within a species" (p. 120).

and Stansfield (2013) mean this when they speak of “geographic origins.” Thus a member of their “Asian” or “Mongoloid” race whose family relocated to Brazil and then back to Japan would not be double-raced merely on account of their double geographic origin. However, the authors’ meaning is unclear.

1.2. *Semiotic ambiguity, subspecies, and a concept needed*

In *Origin of Species* (1859, 51), Darwin recognized that there exists a continuum running from individual variation to species and that hereditary varieties fell along this. He tells us:

Certainly no clear line of demarcation has as yet been drawn between species and sub-species... or, again, between sub-species and well-marked varieties, or between lesser varieties and individual differences. These differences blend into each other by an insensible series; and a series impresses the mind with the idea of an actual passage.

Darwin recognized that both adaptation and isolation were important factors in what he recognized as the process of speciation. Between species and individual variants, Darwin recognized subspecies, “forms which possess many of the characteristics of true species, but which hardly deserve so high a rank” (*Descent of Man*, 1871, 227) and (constant) varieties, for which a “community of descent is almost universally implied, though it can rarely be proved” (*Origin of Species*, 1859, 44). Darwin situated these communities of descent in his genealogy-based classificatory system. As he notes:

In confirmation of this view, let us glance at the classification of varieties, which are believed or known to have descended from one species. These are grouped under species, with sub-varieties under varieties; and with our domestic productions, several other grades of difference are requisite, as we have seen with pigeons. The origin of the existence of groups subordinate to groups, is the same with varieties as with species, namely, closeness of descent with various degrees of modification.... In classing varieties, I apprehend if we had a real pedigree, a genealogical classification would be universally preferred; and it has been attempted by some authors. For we might feel sure, whether there had been more or less modification, the principle of inheritance would keep the forms together which were allied in the greatest number of points.... If it could be proved that the Hottentot had descended from the Negro, I think he would be classed under the Negro group, however much he might differ in colour and other important characters from negroes. (*Origin of Species*, 1859, 426-427)

This extended passage is interesting for several reasons. First, Darwin has in mind a descent-based hierarchical scheme of classifications of organisms which extends well below the level of subspecies, a system of classification which blurs insensibly into individual differences, the raw material for the production of varieties. Second, he understands subspecies to be lineage-based divisions which “come very near to” species. While similar to contemporary taxonomic understandings, insofar as “subspecies” expresses a “taxonomically significant” magnitude of divergence, this conception is markedly different from original ones, as the term *subspecies* was originally employed to describe infraspecific constant varieties in general. For example, defining the term in *Hannoversches Magazin* (1784), Swiss botanist Jakob Ehrhart notes:

Halbarten, Scheinarten, Subspecies.

In this way I term plants which agree in essentials almost completely with each other, and are often so similar to each other that an inexperienced person has trouble in separating them, and about which one can conjecture, not without reason, that they have formally had a common mother, notwithstanding that they now always reproduce their like from seed. They are in a word, Varieties constantes, or an intermediate between *species* and *Spielarten* [inconstant varieties]. They are separated from species in that they differ from one another in small particulars of little importance; and they differ from *Spielarten* in that they reproduce themselves unchanging by seed and always beget their like. (qtd. in Chater, Brummitt & Ehrhart, 1966)

According to Ehrhart, subspecies were varieties which passed on their often minor character differences through their seed, which is to say *constant varieties* or the same type of entities which Comte de Buffon referred to as the *racés* of a species.²⁸ It was only in the mid-19th to early 20th century – and so largely for convenience sake – that *subspecies* came to refer to constant varieties which were more like species in terms of the degree of differentiation, that is, to “the highest grade of variety” (Gray 1879, 321). During the 20th century, *race*, for the most part, was delimited such to refer to infraspecific descent-based divisions in general, thus including both subspecific and infrasubspecific divisions but excluding specific ones. As such, in line with Mayr and Ashlock (1991), King,

²⁸ For example, Buffon (1778, 252), equating infraspecific races with constant varieties, notes: “Races in each species of animal are only constant varieties that are perpetuated by generation, whereas in vegetable species there are no races, no varieties fairly constant to be perpetuated by reproduction.”

Mulligan, and Stansfield (2013) define *subspecies* to mean formally recognized races – ones assigned a trinomen and so treated as taxa.

What is germane is that during the 19th century, the Linnaean conception of variety – and species – was rejected, and that through the mid-19th to the early 20th century, *subspecies* replaced *variety* as the designation for the taxa immediately below species in both botany and zoology. In zoology, unlike botany, no infrasubspecific category came to be recognized. Nonetheless, during the same period, zoological *races* below the level of subspecies were recognized, not formally as part of, to use Kant's phrase, a "systematic description or nature" but as biological classifications, or systematic units, used to understand biological variation (Simpson, 1969;²⁹ Wright, 1978³⁰). Today, Darwin's infrasubspecific varieties would often be, ambiguously, called *populations*. Since *population* can mean geographic population and breeding populations, and since neither of such type of divisions necessarily need to be communities of descent, an important concept, for understanding biological variation, is presently missing. Given this situation, in conjunctions with the difficulty in precisely delimiting specific, subspecific, and infrasubspecific boundaries (Darwin 1859; 1871; Mayden 1997; Mayr 2000), a general concept to describe lineage-based variations, or communities of descent, would be useful.

Regarding such a general concept, Beatty (1985, 278) points out that Darwin treated species and hereditary varieties as the same kind of entity. He notes and asks:

They were referring, Darwin believed, to chunks with[in] the genealogical nexus of life. They did not refer to *one kind* of chunk with their species names and to *another kind* of chunk with their variety names.

²⁹ Simpson (1969, 101-102) notes: "In biology the term "race" is not a systematic category but it is used for any local infraspecific breeding group that is conveniently distinguished for purposes of a given study. The term "subspecies" is used in the technical sense for a race considered sufficiently distinct, uniform, and widespread to merit a Latin name... However, there are many smaller groups which cannot be assigned in a really valid way to one of these major divisions, and it is equally good biology to apply the term race loosely to such groups of all sizes and degrees of distinction."

³⁰ Wright (1978, 439) notes: "There is also no question, however, that populations that have long inhabited separated parts of the world should, in general, be considered to be of different subspecies by the usual criterion that most individuals of such populations can be allocated correctly by inspection... It is, however, customary to use the term *race* rather than subspecies for the major subdivisions of the human species *as well as for minor ones.*" [Italics added.]

This raises the question why Darwin did not at least define a joint "species-variety" category in genealogical terms?

Part of the answer to Beatty's question, one which Beatty himself fails to note, I would suggest, is that Darwin employed the term *race* to refer to this "species-variety" chunk of the genealogical nexus as a *systematic unit*. That is, he was not without a term to describe the concept; he just did not designate a corresponding *taxonomic rank*.

2. The concept of lineage population

One might try to rehabilitate the term *race* – to bring it back in line with its historic meaning of lineage – and then specify a meaning to give it a definite place in contemporaneous phyletic-based systematics. However, the definition of the term is so disputed and riddled with confusion that it is desirable to clarify a needed concept and refer to it by a neutral term. But what is to be described? From the genealogy-based perspective, we notice a type of biological variation in want of a clear concept to pick it out and a minimally ambiguous term to reference this concept. After all, what term describes so-called *Europeans*, what the International HapMap Project refers to as "CEU," living in both Tuscany and Utah, or so-called *East Asians* in the same places? These groups are evidently not spatial populations, and they need not be either breeding populations or species. These are groups of organisms, not characters, whether discontinuous or clinal,³¹ singular or multiple. One might call them *forms* (Štrkalj 2000), but this term is imprecise, not distinguishing between individual variants and populations, and it seems to neglect an important aspect regarding how these groups are delineated. These types of groups will be called *lineage populations*. They are defined as: *intra-fertile* divisions of organisms, where membership is determined by shared ancestry as revealed by ancestry-informative markers, and whose distinctiveness has been maintained by endogamy. In this context, *population* is used in a biostatistical sense – to mean, simply, a group of organisms with some features in common – and is used interchangeably with *division*, *class*, and *variable-type*. If typological thinking simply involves thinking in terms of individual characteristics

³¹ The meaning of the term *cline* shifted over the 20th century. The term originally signified a character gradient – a distribution of traits (Huxley 1939). Referring to this meaning, Simpson (1961, 179) notes: "A cline is an arrangement of characters, not of organisms or of populations." Yet, *cline* has come to be used, often ambiguously, to also describe a population continuum – which is a type of distribution of organisms.

which allow one to classify individuals into groups, this is unabashedly a variable-typological conception as defined by Weiss and Lambert (2011).

In biology, the term is often used to describe cell clonal lineages, but it is also used, at times, to characterize the type of groups being discussed.³² Since we are looking for a neutral term, the infrequency of term use, with respect to organismic groups, is desirable. The concept of lineage population can be contrasted with those of *phenon*, *variant*, or *morph*, which describe intrapopulational variants (Mayr and Ashlock 1991). The distinction would be similar to that made by Kant (1777) with respect to races and individual varieties such as blondes and brunettes or by Comte de Buffon (1777, 555-565) with respect to races and individual varieties such as albinos. Individual variants do not pick out separate lineages and are thus not separate lineage populations. The lineage population concept further differs from the concept called *form*, a neutral term used to describe individuals, phena (phenotypes within a population), or taxa (Mayr and Ashlock 1991). The concepts differ in that lineage populations, as defined here, do not necessarily refer to conspicuously distinct groups – for they could be molecularly and physiologically distinct³³ – and that forms do not necessarily refer to lineage-based divisions.

More centrally, the concept of lineage population can be juxtaposed with those of spatial and breeding population, both of which also describe groups of organisms. In biology, the term *population* has a number of different meanings (Waples & Gaggiotti 2006). As Schaefer (2006) notes, a “unified population concept remains elusive.” Frequently, the term is used to refer to a *geographic population* defined as “a group of individuals of the same species occupying a particular space at a particular time” (qtd. in Waples and Gaggiotti 2006). For example, when, in *Descent of Man*, Darwin discusses the “population of the United States” (pp. 131) and the “immense mongrel population of Negroes and Portuguese” (pp. 225) in Brazil, he is referring to the geographic sense of the term. Alternatively, *population* is used to mean “a group of interbreeding individuals,” or a *breeding population*. *Populations* can also refer to “collections of individuals that share some biological attributes” (Waples and Gaggiotti 2006), or what are here called *biostatistical populations*.

³² For example: Schrode et al. (2012).

³³ Martin and Hine (2008, 196) define a form as “any distinct variant within a species.” Perhaps for them and others one can have molecular and physiological cluster-forms, in which case lineage populations would be a sort of forms.

Finally, *population* is now frequently used to mean what Aulchenko (2010) refers to as a *genetic population* in the retrospective sense. These are biostatistical populations which are delineated in terms of ancestry-indexing characters. As Aulchenko (2010) notes, the term *genetic population* can also mean breeding population. For example, Robinson (2013, 111) tells us: “Conveniently, a genetic population may be defined as a group of individuals freely interbreeding, the limits of which may be either prescribed or implied.” This ambiguity leads Aulchenko (2010) to distinguish between *genetic populations* in the retrospective and prospective senses. For some, the term *genetic population* seems to imply jointly being a breeding population and a lineage population. For example, Verspoor, Stradmeyer, and Nielsen (2008, 484) define a *genetic population* as “a group of sexually reproducing individuals and their relatives, within which mating is more or less random but among which interbreeding is constrained, so that they constitute a distinct gene pool.” That different genetic populations have distinctly different gene pools owing to linebreeding entails that these are lineage populations. Likewise, Mukherjee (2007, 6) defines a *genetic population* as “a reproductively isolated group of individuals of the same species that share in a common descent or a common gene pool...” Here again genetic populations are lineage populations. However, these definitions seem to stipulate that these populations are, at the same time, breeding populations. As defined in this paper, lineage populations do not *necessarily* have to be breeding ones. To take an extreme case, there could be two reproductively isolated groups between which barriers suddenly, completely collapsed. As a result, one would immediately have one breeding population and two distinct lineage populations. This breeding/lineage population distinction allows for the possibility of *hybrids*, as recently exogamously mating individuals maintain their original lineage population status, despite collectively forming one breeding population; this allows their offspring to be of mixed lineage population.

While it is not clear how common this understanding of *population* is, Fujimura et al. (2010) find that, based on their interviews, genome-wide association study (GWAS) researchers “specify populations based on concepts of genetic ancestry.” If this is a general practice, it would be consistent with Jiménez-Tejada et al.’s (2008) finding that unlike in ecology textbooks, in genetic ones, *population* is rarely defined in the geographic sense. If the term *population* is frequently understood to mean lineage population, one might argue that appending “lineage,” for the sake of clarity, is unnecessary. Yet, that explicitness is needed is indicated by the fact that it is not readily obvious to Fujimura et al. (2010) and other authors, including the present one, when *population* means what is here called *lineage population*. That said, by *lineage population* something

similar to Aulchenko's (2010) retrospective *genetic population* is meant, although genetic relatedness might be operationalized differently.³⁴

To further clarify, this concept does not imply phyletic discontinuity between classes; thus, lineage populations, like 18th and 19th century infraspecific races,³⁵ can be picked out of a continuum formed by primary or secondary intergradation. Darwin recognized that lineages exist in a phyletic continuum. Regarding an evolutionary continuum brought about by the resurrection of forms long past, Darwin (1862, 330-331) notes:

It is due to their absence, and to the consequent wide gaps in the series, *that we are enabled to divide the existing species into definable groups*. If there had been no extinction, there would still have been great lines, or branches, of special development ... but ancient and intermediate forms, very different probably from their present descendants, *would have rendered it utterly impossible to separate by distinct characters...* one great body from [an]other. [Emphasis added.]

His point is that phyletic disjunctions enable, or authorize, one to divide by distinct character biodiversity into definable evolutionary groups. In absence of disjunctions, the lineages still exist; they are merely hidden under a continuum of variation. In this case, distinct lineage populations cannot be objectively picked out any more than distinct colors can from the electromagnetic spectrum. In the same way, given similar circumstances, different geographic and breeding populations cannot be objectively delineated. Nor, under any circumstance, can

³⁴ Aulchenko's (2010) definition suggests using pairwise genetic distance to arrange members; however, one could, alternatively, delineate groups based on distance from population centroids.

³⁵ As Wallace (1864) noted, a lack of discontinuity was one of the common arguments made in defense of the position that various human groups *were* infraspecific as opposed to specific *races*: "In favour of the unity of mankind it is argued that there are no races without transitions to others; that every race exhibits within itself variations of colour, of hair, of feature, and of form, to such a degree as to bridge over to a large extent the gap that separates it from other races. It is asserted that no race is homogeneous; that there is a tendency to vary; that climate, food, and habits produce and render permanent physical peculiarities, which, though slight in the limited periods allowed to our observation, would, in the long ages during which the human race has existed, have sufficed to produce all the differences that now appear. It is further asserted that the advocates of the opposite theory do not agree among themselves; that some would make three, some five, some fifty or a hundred and fifty species of man...."

different temporal species. Nor can subspecific taxa which fall along a population continuum.³⁶ All of these divisions are nonetheless recognized.

In the wild, there is an obvious relation between geographic, breeding, and lineage populations, as for relatively sessile and range-restricted organisms, geographic populations of the same species will often be breeding populations. Since these breeding populations are often closed as opposed to *open* or “freely exposed to gene flow” (Mayr & Ashlock 1991, 142), over time they become lineage populations. Owing to the conceptual covariance, distinctions between types of populations are frequently not made. Nevertheless, these specifications need not coincide, as is the case with many zoo animals around the world. Thus, members of the great northern hippopotamus lineage population might find themselves in zoos in East Asia and North America and in their ancestral homeland. Collectively, they would not form a geographic population in any meaningful sense and they need not form a coherent breeding population.

It might be argued that the lineage population concept, as defined here, is too generic to be of practical use and that something in addition to ancestry and descent, such as the presence of notable physical trait differences, should be required. Since the purpose of this concept is analytic, requiring such differences would be undesirable; doing so would require the definition of a more generic primary concept. Practically speaking, it is hard to believe that the lineage population concept is too generic for biologists and others to use, when these same researchers commonly employ the even more non-specific *population* terminology.

In line with geographic and breeding concepts, both specific and infraspecific groups, however such groups are conventionally distinguished, can be lineage populations. Thus lineage population describes specific, subspecific, and infrasubspecific – local and widespread, domestic and wild – communities of descent. The reason for this inclusive usage is both pragmatic and epistemic. For one, restricting the concept to infraspecific groups would limit its applicability; doing so would also render it asymmetrical with the geographic and breeding population concepts, which typically apply to both infraspecific and specific divisions. Additionally, there are a number of species concepts which differently delimit species (Wilkins 2010). The result is that the species of one concept can

³⁶ Some subspecies concepts, for example the popular evolutionary taxonomists', allow subspecific taxa to be cut from the ends of a continuum (see, for example: Mayr and Ashlock 1991, 50).

be the infraspecific “populations” of another. Thus, for example, Mayr’s biological species concept’s *subspecies* and *geographic races* can be Wheeler and Platnick’s diagnostic phylogenetic species concept’s *species* (Mayr 2000; Platnick 2000). Specifying lineage populations as infraspecific groups would require one to specify a species concept. And doing so would unnecessarily embroil the lineage population concept in the seemingly unending debate on the appropriate definition of species.

2.1. *Alternative terms for lineage populations*

Sometimes, in context to humans, lineage populations are called *ethnic groups*. The term *ethnic group* (“groupe ethnique”) was adopted by Joseph Deniker to refer to communities of individuals delineated in terms of language, religion, and culture and to distinguish these social divisions from zoological ones. According to Deniker, the former communities can be composed of a single zoological group or multiple ones (whether species, varieties, or races), whereas the latter are delineated in terms of somatic resemblance (Deniker 1906, 280-284). However, to avoid the use of the term *race*, *ethnicity* has been adopted to refer to somatically and ancestrally delineated groups (Lieberman et al. 2004; Molnar 2015). This practice seems to have been taken up to some extent and the situation has led to the very confusion which Deniker (1906) was attempting to circumvent (Štrkaj 2005). Owing to both semantic ambiguity and its inapplicability to non-human organisms, the term *ethnic group* is undesirable as a substitute for *lineage population*.

Recently, the term *cluster* has been adopted by some – or adopted as a euphemism for *race* meant roughly in the same way (Kitcher 2007). The problem with *cluster* is that it is ambiguous, since it has several substantially different meanings. A *cluster* can mean the statistical output from a cluster analysis, or it can refer to groups of similar organisms identified by cluster analysis; such clusters can refer to all sorts of groups, such as ones delineated by sex or age (Pigliucci 2013). More often, the term *genetic clusters* refers to organismic groups delineated in terms of ancestry-indexing assemblages of phenotypic and/or molecular characters. These lineage clusters would correspond with lineage populations, insofar as the former reliably delineate the latter, which would only be the case if a sufficient number of characters, with a high phyletic weight,³⁷

³⁷ Phyletic weight refers to the “phyletic information content of the character” (Mayr and Ashlock 1991, 185). Lineage populations can be conceptualized as latent factors, ones which are indexed to one degree of reliability or another by sets of characters. If the

were used. Yet *cluster*, in this lineage cluster sense, has also been taken to refer to lineage populations between which there are historic evolutionary phyletic discontinuities. This is because discontinuities resultant of evolutionary patterns (e.g., vicariance), sampling, or recent migrations allow unsupervised cluster analysis to pick out groups; thus the cluster concept is taken, at times, to imply groups between which there are such discontinuities, and it is assumed that, when dealing with systematic or taxonomic groups, these phyletic discontinuities should result from historic evolutionary processes and not, for example, from sampling.³⁸ Thus, Templeton (2006, 216) tells us that “an isolation-by-distance model with no genetic clusters at all will still have the appearance of genetic clusters...” According to Templeton (2006), *actual* clusters are groups between which there are evolved phyletic discontinuities. As a result of these ambiguities and different readings, terms such as *genetic clusters* or *clusters* are problematic when it comes to describing what are here called *lineage populations*.

In relation to the intent of the lineage population concept, there is also a metaphysical concern with cluster concepts. This can be illustrated using Glasgow’s (2010) racial twin earth thought experiment. Glasgow (2010) asks us to imagine the creation of a racial twin earth in which the species and lineage populations/races thereof are identical in form to those on Earth. Based on this thought experiment, he reasons that lineage cannot be central to the meaning of *race*. Across Earths, Glasgow’s twin “Europeans,” despite being separate creations, would indubitably be arranged into the same biogenomic cluster as Earth Europids. However, as defined here, they would not form the same lineage population – divisions which are *indexed* by clusters of characters but *defined* in terms of descent. Indeed, being the product of different creation events, Earth and twin Earth Europids would represent separate *species* in the 18th century polygenist sense. It is not clear what they would represent in modern phyletic-based systematics.

Yudell et al. (2016) insist that terms such as *ancestry* and *populations*, and not *race*, should be used to describe “human groupings in genetic studies.” For

phenotypic or molecular characters analyzed are unreliable indices of “true ancestry,” one can get clusters which are discordant with the underlying lineage populations.

³⁸ Thus, Templeton (1998) notes that “when a biological race is defined as a distinct evolutionary lineage within a species, the question of race can *only be answered in the context of the recent evolutionary history of the species.*” [Italics added.] By his idiosyncratic concept of *race* and *cluster*, for these to be real, they need to represent lineages between which there are/were historic evolutionary disjunctions.

them, *ancestry* is a “statement about an individual’s relationship to other individuals in their genealogical history.” It is precisely because the desire is to describe *collections* of individuals related in terms of descent that *ancestry* and “process-based” terms and concepts such as *geographic ancestry*, *genetic ancestry*, and *biogeographic ancestry* – are insufficient. Simply put, *ancestry* does not specify groups of organisms, let alone groups delineated in terms of overall ancestry (as opposed to, for example, maternal ancestry). In genetic studies, one is frequently interested in ancestry *with respect to biostatistical populations of a specific sort* – specifically, ones delineated in terms of genetic relatedness or nearness of descent.

The term *geographic ancestry* is additionally problematic since lineage populations are not delineated with respect to the geographic origins of ancestors, per se, but rather with respect to shared ancestry. Only when individuals from roughly the same geographic regions descend from the same linebred populations do they belong to the same lineage populations. As an example of discordance, according to OMB Directive 15, an *Asian* by US census standards is a “person having origins in any of the original peoples of the Far East, Southeast Asia, the Indian subcontinent, and the Pacific Islands,” while *Whites* are “persons having origins in any of the original peoples of Europe, North Africa, or the Middle East” (Registrar, 1997). In some sense, these political divisions are delineated in terms of geographic ancestry, yet they do not form coherent lineage populations as South Asians are more ancestrally related to West Eurasians than to East Asians and Pacific Islanders.

A related but more precise term, used in epidemiology and medical research, is *biogeographic ancestry (BGA)*, a term for which “bio-” qualifies ancestry. Gannett (2014) has detailed the origin of the BGA concept. The term *BGA* was first introduced in Pfaff, Parra and Shriver (2000) to refer to “the component of ethnicity that is biologically determined and can be estimated using genetic markers that have distinctive allele frequencies for the populations in question” Frudakis and Shriver (2003) describe *BGA* as “the heritable component of ‘race’ or heritage” and note that it “is relevant on any scale of resolution” from continental groups down. Shriver and Kittles (2004) flesh out the concept. According to them, *BGA* is the component of personal genetic history indexed by ancestrally informative autosomal markers. Unlike maternal and paternal lineage, indexed by mitochondrial and Y-chromosomal DNA, *BGA* reflects an individual’s overall ancestry with respect to local and continental “population groups” (also called *clusters*, *ancestral groups*, and *ancestral populations*). It is said to reflect the effects of evolutionary factors, such as “isolation by distance,” and barriers that “have all affected human migration and mating patterns in the past,” which

have shaped the present worldwide distribution of genetic variation. As Gannett (2014) notes, Shriver sees the distribution of “genetic variation among people” as continuous and sees this as precluding racial classifications where *race* is apparently seen – contrary to the 18th to early 20st century infraspecific sense – as implying phyletic discontinuities. The reference groups for determining BGA have been called *BGA groups* (e.g., Frudakis & Shriver 2003; Frudakis 2010), though the term *BGA group* or variants of this is not commonly used in the literature. Instead, the reference groups are typically ambiguously just called *populations*. An example of the method used can be seen in Keating et al. (2013). Reference samples were taken from HapMap 3. Principal component analysis, applied to allelic data, was then used to group individuals from these reference samples into major “descent groups.” It is notable that the reference groups are not obviously populations in the geographic or breeding sense. The European one, for example, is a biostatistical class based on individuals from Utah, US and Tuscany, Italy. The commonality of the members, in this case, owes to having descended from a once relatively endogamous, geographically circumscribed breeding population. Delineated this way, they are lineage populations. Yet, in principle, not all lineage populations need to be like this. That is, the lineage population concept is meant to be inclusive. All intrafertile classes – allopatric or sympatric – where members are arranged by propinquity of descent are lineage populations. The BGA group concept, then, represents a narrow specification of the lineage population one.

A reviewer suggested that the term *ancestral population* might be used synonymously with what is here called *lineage population*. This, however, seems not to be the case – see, for example, usages in Savolainen et al. (2002) and Bertoni et al. (2003). Specifically, *ancestral population* is used to mean ‘one of the populations from which this population is derived’ and has meaning only in relation to *derived populations*. *Ancestral population* is doubly problematic insofar as one desires a synonym for lineage population. First, it would be semiotically incorrect to refer to two derived lineage populations as being *ancestral populations*. For example, one might coherently speak of the ancestral population linking gorillas and modern humans, but it would be misleading to refer to these two derived species-level lineage populations as being, with respect to one another, separate *ancestral populations*. Second, it is not clear if *ancestral populations* necessarily correspond with *lineage populations*, or whether they can alternatively correspond with highly genetically heterogeneous spatial populations, as they apparently do in the case of the *ancestral populations* of Bertoni et al.’s (2003) US Latin Americans.

A better substitute term might be *ancestry population*. However, the precise meaning of *ancestry populations* is unclear. From 1980 to 2005, the term seems to have been predominately used by sociologists to refer to populations delineated with respect to geographic origin. Thus, authors speak of, for example, a "Hispanic" ancestry population, where this refers to a class of individuals 'having Latin American origin.' As noted previously, such region of origin delineated groups could correspond with lineage populations but they obviously need not. Between 2006 and 2015, the term has increasingly been used in population genetic and genetic epidemiological studies. However, one still finds references to groups which are apparently delineated in terms of geographic origin – for example, the "Hispanic ancestry population" of Hulgán et al. (2015). It is possible that the term *ancestry population* has come to mean, for most researchers, lineage population, that is, one of a set of divisions into which members are arranged by propinquity of descent. However, authors are frustratingly unclear. Given this situation, instead of imposing a definition on a presently ambiguous term, it is desirable to coin a new term for analytic purposes and then inquire: "Are *ancestry populations*, as meant in context to population genetic research, lineage populations?"

A term proposed by Fuerst (2015) is *natural divisions*, where this refers to divisions into which organisms are arranged by lineage or propinquity of descent (Kant 1777; Darwin 1859). Unfortunately, this term could be taken as implying natural partitions based on phyletic discontinuities. While there are historic precedents for equating ancestry-based arrangements with *natural classifications*, for some, phyletic discontinuities are a prerequisite for the "naturalness" of biological divisions. Gray (1879, 322), for example, notes that "if the species blended as do the colors of the rainbow... there could be no natural foundation for their classification. The multitude of species would render it necessary to classify them, but the classifications would be wholly artificial and arbitrary." For Gray (1879), a natural biological classification entails natural partitions, where nature, as Darwin puts it, enables us "to divide the existing species into definable groups." Following Gray (1879), one could argue that genealogical arrangements into divisions are "not really" natural in absence of sufficient phyletic disjunctions. Thus, the term *natural division* potentially lends itself to confusion.

This notion of lineage population is not new. It corresponds with Darwin's (1859) species and hereditary varieties as "communities of descent." While it is outside the scope of this paper to show this through textual analysis, the idea

recapitulates one historic natural scientific understanding of race.³⁹ Granting that, at a given time, infrasubspecific genetic populations in the retrospective sense, subspecies, and species are most often separate lineage populations, the concept is convenient in that it allows one to circumvent ongoing debates concerning how to distinguish these entities from one another. Moreover, the concept allows one to discuss domestic genetic breeds⁴⁰ under the same term much as the polyseme called *race* once did. The lineage population concept further allows one to tie the previously mentioned concepts to ones, such as BGA group or descent group, used in epidemiology and population genetics.

3. Lineage population concept versus the population lineage concept

As defined here, lineage populations are divisions of organisms into which members are arranged by propinquity of descent. This idea is readily contrasted with geographic and breeding populations, understood as groups where members are arranged in terms of, respectively, spatial proximity and the probability of descendant sharing. This concept primarily views organismic groups horizontally across space, as defined by Stamos (2002), and in line with Darwin's perspective (Stamos 2007). A closely related but subtly different concept is called *population lineage*, which Ereshefsky (1992) defines, with respect to species, as "a single descendant-ancestor sequence of organisms or a group of such sequences that share a common origin." The latter concept places emphasis on descendant-ancestor relationship viewed vertically across time.

³⁹ This might be called the "Darwinian concept" of race, since Darwin most clearly formulated the goal of natural or genealogy-based classifications, ones which had the intent of allowing for inductive potency regarding overall organic resemblance. Following Darwin, *rac*es were often seen as a natural classification in this sense. Thus, for example, in "African Races," Chatelain (1894) notes that: "Many criteria - such as the color, the hair, the form of the skull - have been proposed as bases for the racial classification of mankind. All have been helpful, but none has proved adequate. All are one-sided and artificial, failing to grasp and follow through its ramifications the principle of genealogy which seems to be essential for a natural classification." For a 20th century exposition of this concept, see Brues (1990, 1-7); compare with that in Hooton (1946, 1-2, 447-449).

⁴⁰ Historically, breeds were understood to be groups of animals sharing a common phenotype owing to common ancestry resultant of artificial reproductive isolation and selection; see, for example, the definition of Blyth (1835). However, breeders now make the distinction between "genetic breeds" and "phenotypic breeds," the latter which share a common phenotype but are not necessarily particularly related.

Kevin de Queiroz (1999; 2005; 2011) has most extensively developed a general "population lineage"⁴¹ concept of species, according to which a species is a "separately evolving meta-population lineage" (de Queiroz 2005). He reasons that species are population-level "biological entities whose members propagate themselves to form lineages" (de Queiroz 1999). Thus his species concept is very similar to what Wilkins (2009; 2010) identifies as the common historic species concept, which Wilkins calls the "generative concept": "species has always been thought to mean the generation of similar form. That is, a living kind or sort is that which has a generative power to make more instances of itself" (Wilkins 2009, 232). De Queiroz sees this as a unifying concept; to be general enough to be so it is radically inclusive (for a *species* concept). Despite this, it is nonetheless stipulated that the groups are "separately evolving" and "meta-populations".⁴² The concept then seems to exclude hybridizing and converging population lineages in addition to local ones. If de Queiroz's constraints of being "separately evolving" and a "metapopulation" are lifted, we are left with an even more general concept, de Queiroz's *population-lineage*⁴³, which corresponds with what, in context to natural history, *race*, a polyseme when not a concept, typically seemed to mean in the most general sense, that is, as Gray (1879, 320-321) suggested, a "common designation of any group or collection of individuals whose characters are continued through successive generations, whether permanent variety, subspecies, species, or group consisting of very similar species..."

What is relevant to this discussion is that population lineages need not correspond with lineage populations, whether one is dealing with species or infraspecific divisions. This is because the initial members of a population lineage could be as related to the members of their original parental population lineage as to their descendants. This happens, for example, in the case of chromosomal speciation. For example, Milhomem et al. (2008) find evidence of a cryptic

⁴¹ By "population" he means only a group of organisms.

⁴² A term, he tells us, used "to distinguish species, which are traditionally considered to reside at the higher end of the population-level continuum, from populations at the lower end of the continuum, such as demes and family groups" (de Queiroz, 2007).

⁴³ De Queiroz (1999) indicates that the term *population lineage* can apply to the infraspecific or deme-level: "Lineages at lower levels in this continuum (e.g., demes or deme lineages) often separate and reunite over relatively brief time intervals. Toward the other end of the continuum, lineage separation is more enduring and can even be permanent.... In any case, most authors equate species with lineages toward the latter end of the continuum."

species, the $2n=42$ form of *G. carapo* sensu stricto, which is reproductively isolated – the authors speculate due to chromosomal speciation – from sister geographic populations but for which the authors could find no “evident differences in external morphology, meristics and pigmentation between the two forms.” Presumably, the first few generations of this cryptic species and the sibling species would not represent separate lineage populations – distinguishable based on overall relatedness – but would, nonetheless, represent separate population lineages.⁴⁴ A similar disjunction can be found in historic discussions of *race* understood as constant varieties. Defining *race*, Jean Louis Armand de Quatrefages (1861, 81-82) writes:

But, add the authors that we are here confronting, the differences between these varieties are not very substantial; they only concern unimportant features, such as size, color, etc. – Even though it would be so, even though these differences would be as insignificant as we would like to say, who cares? From the moment they became constant and they pass on by way of inheritance, they are no less real races.

This concept of (infraspecific) race is clearly in line with the generative concept, or at least an infraspecific version of it. However, as with the $2n=42$ form of *G. carapo* sensu stricto, members of de Quatrefages’s (1861) races need not initially be lineage populations. De Quatrefages’s (1861) concept was not an uncommon pre-Darwinian one of infraspecific race. Duchesne (1766, 18), for example, points out that race, “the term employed with reason by Buffon in the *Natural History of Animals*, and which asks to be introduced into that of *Vegetable*,” was needed to describe varieties which propagated their form across generations. Otherwise, “by following Ray’s axiom, which cannot consider constant races as varieties, they are named species” which represents an inappropriate classification (Duchesne 1766, 26). In context to strawberries, Duchesne (1766) notes:

⁴⁴ A similar point is made by Hausdorf (2011) in his discussion of the genotypic-cluster concept of species: “The prediction that species sooner or later form genotypic and phenotypic clusters can be derived from most species concepts. Thus, this is doubtlessly a useful criterion for delimiting provisional species. However, incipient species might not yet be recognizable as distinct clusters based on a random sample of genetic markers. In the case of peripatric speciation, the peripheral species will initially often form a cluster with neighboring populations of the more widespread species so that the more widespread species does not form a genotypic cluster distinct from the peripheral species.”

It is certain today that, if all species are stable, there are also races whose distinctions are constant, although belonging to the same species. The Versailles strawberry that I saw born, and which became the head of a race, puts that fact beyond doubt. Cultivation and other accidental causes do not produce new species, but changes in certain individuals do occur that are perpetuated in their posterity, constituting new races. (Appendix, "Remarques Particulières," pp. 11-21).

We see that *race* as constant variety is explicitly the infraspecific equivalent of Wilkins' generative species concept, discussed above, and like the generative species concept, it is derived from – or more correctly in this case, in context to – Ray's biological species concept, the first modern biological one. The disjunction between the lineage population and population lineage concepts becomes more apparent when examining Duchesne's phylogenetic network of strawberry races. Discussing the birth of "La Race nouvelle," he notes that he observed how the fertilization of a Frutiller female by a male Capiton produced a mix who "will form perhaps a new race" (pp. 223-227). Either the initial head of the Versailles strawberry race, produced by the marriage of le Capiton and le Frutiller, would be of the Versailles strawberry race or its offspring would, assuming that the race continued through either self-fertilization or the incestuous mating of le Capiton and le Frutiller's offspring. In either situation, the initial members of one race would be as related to the members of their original parental race as to their descendent race. Thus, strictly understood, members of constant variety – or generative – races need not form lineage populations.

The reason for the focus on lineage populations is that they are more inductively interesting. To paraphrase Darwin, the physiological and morphological resemblance of lineage populations and their pedigrees generally correspond; thus knowing that two groups are separate lineage populations gives one more inductive leverage than knowing that they are only different population lineages. However, insofar as one is interested in the most inclusive concept of either species or what was called *race*, lineage population would not be it. The lineage population concept is rather, from the perspective of systematics, a specification of a more general concept – what one gets when population lineages are sufficiently linebred.⁴⁵

⁴⁵ It would require some interpretive footwork to make the case that *races* typically picked out population lineages. To give an example of the hermeneutic problem, as Douglas (2005) notes, Buffon (1777, 462-463, 479-484) allows his Lapp race – using the word *race* "in the broadest sense" (pp. 462) -- which he also refers to as a "species" (pp. 480-481) to be polyphyletic, with the Lapp sub-races grouped together on account of their supposed

3.1. *The lineage population concept versus the race as breeding population*

There is substantial semiotic overlap between what is here called *lineage populations* and what were in the 18th and 19th centuries called *races*. This stems from both terms referring to lineage-based groups, whether on the specific or infraspecific level.⁴⁶ For example, Georges Cuvier (1831, 73) defines species as “individuals who descend from one another, or from common parents, and those which resemble them as strongly as they resemble one another” and notes that “we only call the *varieties* of a species, those races, more or less different, which may have proceeded from them by generation.” His races as species were *lineage populations* and his races as varieties were *population lineages* which could also have been lineage populations. As suggested above, though, there are also substantive inconsistencies. This topic is complicated by the existence of a few different primary historical concepts which disagree in important respects and because, during this time, biological variation was approached from very different systematic perspectives.

epigenetically induced overall resemblance. Understood as polyphyletic groups, these would not be population-lineages in Ereshefsky's (1992) sense. Yet, given contemporaneous theory, classifications based on overall resemblance, which Buffon was aiming for, would end up delineating lineage-populations, groups which would be types of population lineages.

⁴⁶ Doron (2011, 763) notes that “the concept of ‘race’ ... refers to genealogically constant differences, inscribed in lines, which make it possible to base a classification. It would be difficult to find an author at the end of the eighteenth, nineteenth century and the first half of the twentieth century who did not accept this definition of the concept of ‘race’.” This statement needs some amending. *Race* qua *constant variety* and qua *species* was doubly used to refer to genealogically constant differences and to the lines of descent along which these were transmitted. Yet, the term was also used to refer to lines of descent which had no determinate relation to differences, thus, for example, the polygenists’ infraspecific *races* as *Linnaean varieties*. The common idea across early usages was lineage, as one might anticipate based on the term’s etymology. In contrast, the term *species* was understood to imply “genealogically constant differences” – or different forms which reproduced themselves. Discussing the terms, Smith (2015, 143) cogently notes: “‘Species’ occupied a distinct but nonetheless partially overlapping semantic field with ‘race,’ to the extent that the former term, as its etymology suggests, was concerned with the external aspect or appearance of a creature... The principal semantic difference between ‘species’ and ‘race,’ where these in fact differed, had to do with the fact that the former focused on physical traits of creatures, while the latter also recalled to mind the lineage or generative series from which – to return to the deepest etymology of the term – these traits flow.”

Certain 20th century concepts of race at times diverge more substantially from the lineage population one – specifically, concepts which identify races with breeding populations and do not imply (e.g., by also identifying them with reproductive isolates) lineage-based groups. For example, Strkalj (2000) tells us that race either means breeding population or subspecies in Mayr’s sense.⁴⁷ He suggests further that the term *race*, as typically used in context to biological anthropology, is redundant with the term *breeding population*. What he means by *breeding population* is not clear, but he references the work of Stephen Molnar (1998).

Molnar (2015, 18), in the sixth edition of the book referenced above, recognizes that, historically, *race* was used to refer to “breeds of domestic animals – their groups membership or descent from a common ancestor.” Strangely, despite recognizing the historic relation between the notions of race and descent, lineage does not take a prominent role in the conception. After reviewing a few concepts, he notes that there are numerous definitions which seem to agree little except with regards to two common components: an assumption about geography in the formation of races and a placing of importance on “breeding populations.” Conveniently, in his glossary, he defines *breeding population*: a “group of individuals who are potentially interbreeding, who occupy a local area, and who make up a basic unit in our species” (p. 420). In light of his conceptual analysis, he decides to use *race* sparingly to mean “a label we append to a population grouping with some physical characteristics that have some genetic component” (p. 398). By this definition, *races* seemingly could be different breeding and geographic populations which happen to, on average, genetically differ in a number of traits. Read literally, ancestrally-heterogeneous North American and Western European residents could collectively represent two different races. Molnar makes it clear that the intent of this understanding is to “appreciate the fluidity of boundaries due to human behavior” (pp. 317-318) His conception seems to accomplish that task by departing greatly from the typical 18th and 19th century lineage-based understanding of *race*.

Of course, the relation between his sense of *race* and ancestry is noticed. For example, he tells us that to replace the term *races*, “ethnic groups” is “more

⁴⁷ In discussing subspecies, he refers to Mayr’s definition. But then he states that the question is whether one can “make a meaningful grouping within the species *Homo sapiens* above the level of breeding populations.” A logical asymmetry is involved in the question because the *breeding population* systematic classification is not a level in the way that Mayr’s subspecies category is a taxonomic rank.

and more frequently used today as a substitute term for people presumed to be of different ancestral descent..." (p. 309). Likewise, the relation between his sense of *race* and genetic clusters is recognized, since we are told, after he cites the work of Cavalli-Sforza, that what had "once appeared to be a few simple subdivisions of our species turns out to be numerous small and large clusters of genetic heterogeneous groups" (p. 310). One would think that the recognition of the relation between *race* and ancestry and *race* and groups arranged by phyletic-informative clusters of characters would bring to Molnar's mind a different historic race concept – and lead to a different definition. This appears not to be the case. The objective here is not to pick apart Molnar's discussion but to illustrate, again, how the lineage population concept differs from some contemporary and historical race concepts and how some contemporaneous race concepts are often rather opaque, unspecific, and not clearly related to historic lineage-based ones.

4. Conclusion

Yudell et al. (2016) have recently argued that *race* should be taken out of population genetics. Briefly, they see *race* as problematic because as a polyseme it has inconsistent definitions, and as a network of concepts it refers to a taxonomic categorization "based on common hereditary traits" for the purposes of clarifying "the relationship between our ancestry and our genes" and is "pattern-based." They proposed that alternative terms such as *ancestry* and *population* should be used to describe human groups because "the scientific language of race has a considerable influence on how the public (which includes scientists) understands human diversity."

Their second criticism makes little sense since, as Kant (1788) noted over 200 years ago, "the word is not to be found in a[ny] systematic description of nature," that is, the term *race* does not refer to a formal zoological or botanical taxonomic category. Instead, terms such as *genus*, *species*, and *subspecies/variety* did and do. Historically, in context to natural history, *race* simply referred to lineage. Insofar as taxa, and other groups such as domestic breeds and infrasubspecific varieties, were understood to be these, they were called *races*. Thus one could speak of the human race (lineage), the Tartar race (lineage), or a particular race (lineage) of poultry or strawberries. As for their third criticism, "pattern based" seems simply to mean "class based" – to refer to groups defined in terms of patterns of traits. This is a strange criticism since the authors apparently have no problem with the same types of groups traveling under the name of *genetic population* and presumably *BGA group*. The opposition, in this regards, seems to be not to "pattern-based" concepts, per se, but to a word which

connects dense conceptual networks to the sanitized “pattern-based” concepts which they feel more comfortable using.

Regardless, it cannot be denied that *race*, the term, especially presently, suffers from having multiple, inconsistent, and disputed definitions. And yet there is nonetheless something in nature to be described, which the term, however ambiguously, used to. A clearly articulated, unifying concept is needed to fully understand biological variation in line with the Kantian/Darwinian principle for natural history – a concept of specific and infraspecific divisions of organisms arraigned in terms of propinquity of descent. By assigning the neutral term, *lineage population*, to this concept, future misconceptions are avoided. With this analytic concept on hand, it can be investigated if concepts referenced by other more frequently used terms have identical meanings.

Some limitations of the concept are worth reiterating. While the lineage population construct is useful, as testified by the number of studies which employ closely related and overlapping constructs, not all lineage-based variation is captured by the concept. Hausdorf (2011) has made a similar point regarding the genotypic-cluster concept of species in context to discussion of a general species concept. In particular, not all “biological entities whose members propagate themselves to form lineages” (de Queiroz 1999) are captured by the concept. As such, some of the entities which historically were called *rac*es are unidentified by this concept.

References

- Allaby, M. (2013). *A Dictionary of Geology and Earth Sciences*, 4th edition. Oxford Univ. Press.
- Aulchenko, Y.S. (2010). Effects of population structure in genome-wide association studies. *Analysis of Complex Disease Association Studies: A Practical Guide* 123.
- Beatty, John. (1985). Speak of Species: Darwin's Strategy. In: David Kohn (ed.), *The Darwinian Heritage*, pp. 265-282. Princeton: Princeton University Press.
- Beeton, S. (1871). *Beeton's Dictionary of Natural History*. London: Ward, Lock & Tyler.
- Bertoni, B., Budowle, B., Sans, M., Barton, S.A. & Chakraborty, R. (2003). Admixture in Hispanics: Distribution of ancestral population contributions in the Continental United States." *Human Biology* 75: 1-11.
- Blumenbach, J.F. (1825). *A Manual of the Elements of Natural History*. London: W. Simpkin & R. Marshall.

- Blyth, E. (1835). An attempt to classify the "varieties" of animals, with observations on the marked seasonal and other changes which naturally take place in various British species, and which do not constitute varieties." *Magazine of Natural History* 8: 40-53.
- Bowler, P.J. (1989). *Evolution: The History of an Idea*. Univ. of California Press.
- Bory de Saint-Vincent, J.B. & Marcellin, M.J.B.G (1827). *L'Homme (homo): Essai zoologique sur le genre humain*. Paris: Rey et Gravier.
- Boyd, W.C. (1950). *Genetics and the Races of Man: An Introduction to Modern Physical Anthropology*. Boston: Little, Brown & Co.
- Brace, C.L. (1964). On the race concept. *Current Anthropology* 5: 313-320.
- Broca, P. & Blake, C.C. (1864). *On the Phenomena of Hybridity in the Genus Homo*. London: Longmans, Green & Co.
- Brues, A.M. (1990). *People and Races*. MacMillan Publishing Co.
- Buffon, G.L.L. (1777). *Histoire naturelle générale et particulière, servant de suite à l'histoire naturelle de l'homme: supplément*, Tome quatrième. Paris: Impr. royale.
- Buffon, G.L.L. (1778). *Histoire naturelle générale et particulière, servant de suite à l'histoire naturelle de l'homme: supplément*. Tome cinquième. Paris: Impr. royale.
- Chatelain, H. (1894). African races. *Journal of American Folklore* 7(27).
- Chater, A.O., Brummitt, R.K. & Ehrhart, F. (1966). Subspecies in the works of Friedrich Ehrhart. *Taxon* 15: 95-106.
- Cotgrave, R. (1611). *A Dictionarie of the French and English Tongues*. London: Adam Islip.
- Cuvier, G. (1831). *A discourse on the revolutions of the surface of the globe, and the changes thereby produced in the animal kingdom*. Philadelphia: Carey & Lea.
- Darwin, C. (1859). *On the Origin of Species by Means of Natural Selection, or The Preservation of Favoured Races in the Struggle for Life*. London: Murray.
- Darwin, C. (1862). *On the Various Contrivances by Which British and Foreign Orchids are Fertilised by Insects: And on the Good Effects of Intercrossing*. London: J. Murray.
- Darwin, C. (1871). *The Descent of Man*, 2 Vols. London: J. Murray.
- Darwin, C. (1903). *More Letters of Charles Darwin: A Record of His Work in a Series of Hitherto Unpublished Letters*, Vol. 2. New York: Appleton.
- Deniker, J. (1906). *The Races of Man: An Outline of Anthropology and Ethnography*. London: W. Scott.
- De Quatrefages, A. (1861). *Unité de l'espèce humaine*. L. Hachette.

De Queiroz, K. (1999). The general lineage concept of species and the defining properties of the species category. In: R.A. Wilson (ed.), *Species: New Interdisciplinary Essays*, pp. 49-89. Cambridge, MA: MIT Press.

De Queiroz, K. (2005). Different species problems and their resolution. *BioEssays* 27: 1263-1269.

De Queiroz, K. (2007). Species concepts and species delimitation. *Systematic Biology* 56: 879-886.

De Queiroz, K. (2011). Branches in the lines of descent: Charles Darwin and the evolution of the species concept. *Biological Journal of the Linnean Society* 103(1): 19-35.

Doron, C.O. (2011). *Races et dégénérescence. L'émergence des savoirs sur l'homme anormal*. PhD diss., Université Paris-Diderot-Paris VII.

Doron, C.O. (2012). Race and genealogy: Buffon and the formation of the concept of 'race.' In: E. Casetta & V. Tripodi (eds.), *Making Sense of Gender, Sex, Race, and the Family. Humana Mente Journal of Philosophical Studies* (22): 75-109.

Douglas, B. (2005). Notes on 'race' and the biologisation of human difference. *Journal of Pacific History* 40: 331-338.

Duchesne, A.N. (1766). *Histoire naturelle des fraisières*. Paris: Didot le jeune.

Ereshefsky, M. (1992). Eliminative pluralism. *Philosophy of Science* 59: 671-690.

Forster, G. (1786). *Something More About the Human Races*, translated by Jon Mikkelsen. SUNY Press, 2013.

Frudakis, T. (2010). *Molecular Photofitting: Predicting Ancestry and Phenotype Using DNA*. Elsevier.

Frudakis, T. & Shriver, M. (2003). Compositions and methods for inferring ancestry. U.S. Patent Application 10/644,594, filed August 19.

Fuerst, J. (2015). The nature of race: The genealogy of the concept and the biological construct's contemporaneous utility. *Open Behavioral Genetics*.

Fujimura, J.H., Rajagopalan, R., Ossorio, P.N. & Doksum, K. (2010). Race and ancestry: Operationalizing populations in human genetic variation studies. In: I. Whitmarsh & D.S. Jones (eds.), *What's the Use of Race? Modern Governance and the Biology of Difference*, pp. 170-183. Cambridge, MA: MIT Press.

Gannett, L. (2014). Biogeographical ancestry and race. *Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences* 47: 173-184.

Girtanner, C. (1796). *Concerning the Kantian Principle for Natural History*, translated by Jon Mikkelsen. Albany: SUNY Press, 2013.

Glasgow, J. (2010). *A Theory of Race*. Routledge.

Gould, G. (1894). *An Illustrated Dictionary of Medicine, Biology and Allied Sciences*. Philadelphia: P. Blakiston Son & Co.

Gray, A. (1879). *Structural Botany: Or Organography on the Basis of Morphology. To Which is Added the Principles of Taxonomy and Phytography, and a Glossary of Botanical Terms*, Vol. 1. New York: American Book Co.

Hausdorf, B. (2011). Progress toward a general species concept. *Evolution* 65: 923-931.

Hochman, A. (2013). Racial discrimination: How not to do it. *Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences* 44(3): 278-286.

Hooton, E.A. (1946). *Up from the Ape*. New York: Macmillan.

Hulgan, T., Samuels, D.C., Bush, W., Ellis, R.J., Letendre S.L., Heaton, R.K., Franklin, D.R. et al. (2015). Mitochondrial DNA haplogroups and neurocognitive impairment during HIV infection. *Clinical Infectious Diseases* 61: 1476-1484.

Huxley, J.S. (1939). Clines: An auxiliary method in taxonomy. *Bijdr. Dierk* 27(5): 491-520.

Jevons, W.S. (1874). *The Principles of Science: A Treatise on Logic and Scientific Method*, Vol. 1. London: Macmillan.

Jiménez-Tejada, M.-P., Hódar, J.A., González-García, F. & Naranjo, J.A. (2008). Population and species concepts in conservation biology and their treatment in textbooks of ecology and genetics. In: *Biological Sciences Ethics and Education: The Challenges of Sustainable Development. Proceedings of the BioEd 2008 Conference*.

Kant, I. (1777). *On the Different Human Races*, translated by Jon Mikkelsen. Albany: SUNY Press, 2013.

Kant, I. (1785). *Determination of the Concept of a Human Race*, translated by Jon Mikkelsen. Albany: SUNY Press, 2013.

Kant, I. (1788). *On the Use of Teleological Principles in Philosophy*, translated by Jon Mikkelsen. Albany: SUNY Press, 2013.

Keating, B., Bansal, A.T., Walsh, S., Millman, J., Newman, J., Kidd, K., Budowle, B. et al. (2013). First all-in-one diagnostic tool for DNA intelligence: Genome-wide inference of biogeographic ancestry, appearance, relatedness, and sex with the Identitas v1 Forensic Chip. *International Journal of Legal Medicine* 127: 559-572.

King, R.C., Mulligan, P. & Stansfield, W. (2013). *A Dictionary of Genetics*, 8th edition. London: Oxford Univ. Press.

Kitcher, P. (2007). Does 'race' have a future? *Philosophy & Public Affairs* 35(4): 293-317.

Lenoir, T. (1980). Kant, Blumenbach, and vital materialism in German biology. *Isis* 71(256): 77-108.

Lieberman, L. (1968). The debate over race: A study in the sociology of knowledge. *Phylon* 29: 127-141.

Lieberman, L. & Reynolds, L. (1978). The debate over race revisited: An empirical investigation. *Phylon* 39(4): 333-343

Lieberman, L., Kirk, R.C. & Corcoran, M. (2000). The decline of race in American physical anthropology. *Anthropological Review* 66: 3-21.

Lieberman, L., Kaszycka, K.A., Martinez, A.J., Yablonsky, F.L., Kirk, R.C., Štrkalj, G., Wang, Q. & Sun, L. (2004). The race concept in six regions: Variation without consensus. *Collegium Anthropologicum* 28(2): 907-921.

Littlefield, A., Lieberman, L., Reynolds, L.T., Azevêdo, E.S., Beals, K.L., Brace, C.L., Garn, S.M. et al. (1982). Redefining race: The potential demise of a concept in physical anthropology [and comments and reply]. *Current Anthropology* 23: 641-655.

Martin, E. & Hine, R. (2008). *A Dictionary of Biology*, 6th ed. Oxford: Oxford University Press.

Maupertuis, P.L.M. de (1745). *Venus physique*. In *Oeuvres*. Lyon: Bruyset, 1768.

Mayden, R.L. (1997). A hierarchy of species concepts: The denouement in the saga of the species problem. In: M.F. Claridge, H.A. Dawah & M.R. Wilson (eds.), *Species: The Units of Biodiversity*, pp. 381-423. London: Chapman & Hall.

Mayr, E. (2000). A defense of the biological species concept. In: Q.D. Wheeler & R. Meier (eds.), *Species Concepts and Phylogenetic Theory: A Debate*, pp. 161-166. New York: Columbia Univ. Press.

Mayr, E. (2002). The biology of race and the concept of equality. *Daedalus* 131(1): 89-94.

Mayr, E. & Ashlock, P.D. (1991). *Principles of Systematic Zoology*. New York: McGraw-Hill.

Mayr, E. & Bock, W.J. (2002). Classifications and other ordering systems. *Journal of Zoological Systematics and Evolutionary Research* 40(4): 169-194.

Milhomem, S.S.R., Pieczarka, J.C., Crampton, W.G.R., Silva, D.S., De Souza, A.C.P., Carvalho, J.R. & Nagamachi, C.Y. (2008). Chromosomal evidence for a putative cryptic species in the *Gymnotus* scarapo species-complex (Gymnotiformes, Gymnotidae). *BMC Genetics* 9(1): 1.

Molnar, S. (1998). *Human Variation: Races, Types, and Ethnic Groups*. New York: Prentice Hall.

- Molnar, S. (2015). *Human Variation: Races, Types, and Ethnic Groups*. New York: Routledge.
- Montague, A. (1942). *Race: Man's Most Dangerous Myth*. New York: Columbia Univ. Press.
- Mukherjee, D.P. (2007). *Outline of Population Genetics*, Vol. 1. Allied Publishers.
- Müller-Wille, S. (2007). Figures of inheritance, 1650–1850. In: S. Müller-Wille & H.J. Rheinberger (eds.), *Heredity Produced: At the Crossroads of Biology, Politics, and Culture, 1500–1870*, pp. 35-42. Cambridge, MA: MIT Press.
- Noël, F.J.M. & Chapsal, C.P. (1832). *Nouveau dictionnaire de la langue française*. Paris: Roret.
- O'Brien, S.J. & Mayr, E. (1991). Bureaucratic mischief: Recognizing endangered species and subspecies. *Science* 251: 1187-1188.
- Pfaff, C.L., Parra, E.J. & Shriver, M.D. (2000). Genetic estimation of biogeographical ancestry. *American Journal of Human Genetics* 67: 221-221.
- Pigliucci, M. (2013). What are we to make of the concept of race? Thoughts of a philosopher–scientist. *Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences* 44(3): 272-277.
- Platnick, N.I. (2000). A defense of the phylogenetic species concept (sensu Wheeler and Platnick). In: Q.D. Wheeler & R. Meier (eds.), *Species Concepts and Phylogenetic Theory: A Debate*, pp. 185-197. New York: Columbia Univ. Press.
- Prichard, J.C. (1836). *Researches into the Physical History of Mankind*, Vol. 1. London: Sherwood, Gilbert & Piper.
- Registrar, Federal (1997). Revisions to the standards for the classification of federal data on race and ethnicity. *Federal Registrar* (62): 58781-58790.
- Richelet, P. (1757). *Nouveau dictionnaire françois*. Geneve: G. de Tournes.
- Robinson, R. (2013). *Lepidoptera Genetics: International Series of Monographs in Pure and Applied Biology: Zoology*, Vol. 46. Oxford: Elsevier.
- Rycaut, P. (1668). *The Present State of the Ottoman Empire*. London: Starkey & Brome.
- Savolainen, P., Zhang, Y.-P., Luo, J., Lundeberg, J. & Leitner, T. (2002). Genetic evidence for an East Asian origin of domestic dogs. *Science* 298: 1610-1613.
- Schaefer, J.A. (2006). Towards maturation of the population concept. *Oikos* 112(1): 236-240.
- Schrode, K.M., Ward, J.L., Vélez, A. & Bee, M.A. (2012). Female preferences for spectral call properties in the western genetic lineage of Cope's gray treefrog (*Hylachrysolcelis*). *Behavioral Ecology and Sociobiology* 66: 1595-1606.

Shriver, M.D. & Kittles, R.A. (2004). Genetic ancestry and the search for personalized genetic histories. *Nature Reviews Genetics* 5: 611-618.

Simpson, G.G. (1961). *Principles of Animal Taxonomy*. New York: Columbia Univ. Press.

Simpson, G.G. (1969). *Biology and Man*. New York: Harcourt, Brace & World, Inc.

Smith, J.E.H. (2015). *Nature, Human Nature, and Human Difference: Race in Early Modern Philosophy*. Princeton: Princeton University Press.

Stamos, D.N. (2002). Species, languages, and the horizontal/vertical distinction. *Biology and Philosophy* 17(2): 171-198.

Stamos, D.N. (2005). Pre-Darwinian taxonomy and essentialism—A reply to Mary Winsor. *Biology and Philosophy* 20: 79-96.

Stamos, D.N. (2007). *Darwin and the Nature of Species*. Albany: SUNY Press.

Štrkalj, G. (2000). Form and race: Terminological concepts for the study of human variation. *Mankind Quarterly* 41: 109-118.

Štrkalj, G. (2005). Ideological historiography in biological anthropology: Deniker, Montagu and 'ethnic group'. *International Journal of Humanistic Studies* 4: 34-44.

Templeton, A.R. (1998). Human races: A genetic and evolutionary perspective. *American Anthropologist* 100: 632-650.

Templeton, A.R. (2006). *Population Genetics and Microevolutionary Theory*. Hoboken, NJ: John Wiley & Sons.

Verspoor, E., Stradmeyer, L. & Nielsen, J.L. (eds.) (2008). *The Atlantic Salmon: Genetics, Conservation and Management*. Oxford: Blackwell.

Virey, J.J. (1837). *Natural History of the Negro Race*. Charleston: DJ Dowling.

Wagner, J.K., Yu, J.-H., Ifekwunigwe, J.O., Harrell, T.M., Bamshad, M.J. & Royal, C.D. (2016). Anthropologists' views on race, ancestry, and genetics. *American Journal of Physical Anthropology* 162: 318-327.

Wallace, A.R. (1864). The origin of human races and the antiquity of man deduced from the theory of natural selection. *Journal of the Anthropological Society of London* 2: clviii-clxxxvii.

Waples, R.S. & Gaggiotti, O. (2006). Invited Review: What is a population? An empirical evaluation of some genetic methods for identifying the number of gene pools and their degree of connectivity. *Molecular Ecology* 15: 1419-1439.

Weiss, K.M. & Lambert, B.W. (2011). When the time seems ripe: Eugenics, the Annals, and the subtle persistence of typological thinking. *Annals of Human Genetics* 75: 334-343.

Wilkins, J.S. (2009). *Species: A History of the Idea*, Vol. 1. Berkeley: Univ. of California Press.

Wilkins, J.S. (2010). How many species concepts are there? *The Guardian*, London.

Wright, S. (1978). *Evolution and the Genetics of Populations, Volume 4. Variability Between and Among Natural Populations*. Chicago: University of Chicago Press.

Yudell, M., Roberts, D., DeSalle, R. & Tishkoff, S. (2016). Taking race out of human genetics. *Science* 351: 564-565.