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Charles Darwin, The First Paleoanthropologist

In *The Descent of Man and Selection in Relation to Sex* (1871), Charles Darwin extended and broadened his earlier ideas about evolution to a degree that has not been fully appreciated. Stating that he had over emphasized the role of natural selection in his 1859 publication, *On the Origin of Species by Means of Natural Selection*, Darwin expanded his theory to include many, if not most, of the concepts that inform contemporary evolutionary biology. Some of his ideas anticipated the emerging fields of evolutionary developmental biology (evo-devo) and epigenetics. Darwin discussed the potential of certain pathological conditions (such as microcephaly) for providing insights about human evolution, which is only beginning to be explored by modern geneticists. He correctly predicted the discovery of a hominin fossil record, including its African origin and its transitional morphology (i.e., between apes and humans). Darwin believed that sexual selection played an important role in the emergence of global human variation, which is probably his most neglected contribution, perhaps because the term he used ("race") is currently avoided by many paleoanthropologists and social scientists. Darwin believed that humans became the dominant species on earth because of advanced intellectual abilities that facilitated the evolution of language. Darwin's prescient ideas about human evolution set the stage for the emergence of paleoanthropology.

KEY WORDS: *Charles Darwin, epigenetics, hominin evolution, race, sexual selection.*

Although Charles Darwin (1809-1882) had pondered human evolution for many years, he was determined not to publish his ideas on the subject because he feared that, to do so, would "only add to the prejudices against my views" (Darwin, 1871, I:1). His observations regarding human evolution were therefore minimal in *On the Origin of Species by Means of Natural Selection* (1859), in which he simply predicted that the evolutionary forces that acted on other organisms would eventually shed light on "the origin of man and his history" (Darwin, 1871, I:1). Twelve years after *Origin of Species* was published, Darwin capitulated because, by then, a large number of up-and-coming naturalists had embraced his evolutionary hypotheses. He, thus, published his ideas about human evolution in a two-volume set, *The Descent of Man and Selection in Relation to Sex* in 1871. It is an illuminating read.

Because Darwin's knowledge about plants and animals was extensive, he was able to compare a multitude of extant organisms from various parts of the world and compare fossils with each other and with living forms. From these data, he detected general patterns and made evolutionary inferences (i.e., he used inductive reasoning). As Darwin

pointed out in the Introduction to *Descent of Man*, it was not until 1871 that he first applied his evolutionary ideas to the study of only one species— "man". What has not been adequately appreciated is the degree to which Darwin extended and broadened his earlier ideas about evolution when he finally focused on humans. For example, the suggestion that he emphasized natural selection to the detriment (if not neglect) of other evolutionary forces needs tempering in light of his more developed observations:

> In the earlier editions of my 'Origin of Species' I probably attributed too much to the action of natural selection or the survival of the fittest. I have altered the fifth edition…I had not formerly sufficiently considered the existence of many structures which appear to be…neither beneficial nor injurious….I was not able to annul the influence of my former belief, then widely prevalent, that each species had been purposely created; and this led to my tacitly assuming that every detail of structure, excepting rudiments, was of some special, though unrecognized, service. (Darwin, 1871, I:152-153)

The fact that Darwin was unaware of the genetic research of Austrian monk Gregor Mendel (1822-1884) has frequently been lamented, as has the less well-known fact that, despite having read *Origins of Species*, Mendel apparently failed to see the connection between his discoveries and Darwin's (Hayden, 2009). Although Darwin did not know what a gene was, he recognized that traits were sometimes "transmitted through two, three, or many generations, and are then under certain unknown favourable conditions developed" (1871, I:280), which he attributed to reversions (see below). In his famous pea experiments, Mendel determined that such transmission and expression of traits, at least in certain hybrid generations, could be explained by the principles of dominance and recessiveness.

Despite his lack of genetics, Darwin discussed a surprisingly large number of the evolutionary concepts that are a mainstay of contemporary evolutionary biology, genetics, and evolutionary psychology. In addition to evolutionarily neutral traits described in the above quotation, and although he used terminology that sounds odd to modern ears, by the time Darwin turned his attention to humans he recognized, to greater or lesser degrees: evo-devo, the constraint of natural selection on range of variation, reciprocal altruism, high-altitude adaptation, atavisms, pleiotropy, micro versus macro evolution, fixation of traits, [gene] flow, mutations, group selection, social intelligence hypothesis, kin selection, cladistic analysis (or close to it), parallel evolution, branching evolution, exaptation, extinction, clines, island effect (or close to it), female choice, runaway sexual selection, sex-linked traits, and the underpinnings for probable mutation effect [PME]. (See Appendix for details.) Not bad for a beginner. He did not get everything right, of course, but in *Descent of Man* he came closer than I had previously realized.

In some ways, Darwin may actually have been ahead of today's scientists. One instance has to do with the concept that acquired traits may be inherited, famously attributed to Jean-Baptiste Lamarck (1744-1829). The classic example is the long neck

of giraffes that supposedly resulted from initially short-necked individuals stretching to reach for leaves in tall trees. According to the Lamarckian view, the offspring of these giraffes were born with the long necks that their parents had acquired. This contrasts, of course, with Darwinian natural selection, which attributes the evolution of long necks in giraffes to differential survival and reproduction of long-necked compared to shorter-necked individuals. The distinction between Lamarckian and Darwinian explanations is painted so starkly in textbooks that students are often left with the impression that Darwin's thinking was completely anti-Lamarckian. It was not. Darwin, in fact, believed that inheritance of acquired traits contributed partly to evolution. Thus, he wrote, "Natural selection had been the chief agent of change, though largely aided by the inherited effects of habit" (Darwin, 1871, I:152-153).

The burgeoning field of epigenetics ("above genetics") suggests that, to some extent, Darwin and Lamarck were right. Epigenetic factors activate or deactivate genes, but without changing their basic structure. Studies in plants, zebrafish, and rodents have shown that epigenetic modifications that alter gene expression can be acquired during development and, at times, transmitted between generations—a possibility that is currently being explored for humans (Miller, 2010; Petronis, 2010). For example, certain epigenetic modifications that occur in the brains of rat mothers in response to stress appear to be passed to subsequent generations, which acquire the increased sensitivity to stress. Although epigenetic studies reveal that some acquired traits can be passed down to future generations, no one has suggested this happens at a level that affects functional structures that are as dramatic as the long necks of giraffes. It, thus, appears that in addition to genetic mechanism of evolution, a certain amount of "soft inheritance" (Hayden, 2009) of acquired traits seems to occur because of epigenetic mechanisms that broker the interaction between environmental stimuli and the responses to them that occur during development.

Contemporary scientists are also just beginning to catch up with another of Darwin's insights that has to do with some of the traits he identified as "reversions," known to us as atavisms or, more commonly, evolutionary throwbacks. Darwin distinguished reversions from rudimentary organs. For example, he noted that human canines retain rudimentary shape features of the larger projecting canines of apes that, in the latter, are used for "tearing [their] enemies or prey" (Darwin, 1871, I:126). On the other hand, he regarded occasional reports of atypical human skulls with projecting canines that interlocked in an apelike manner as instances of reversions to an ancestral condition. Thus, "whenever a structure is arrested in its development, but still continues growing until it closely resembles a corresponding structure in some lower and adult member of the same group, we may…consider it as a case of reversion…..to some earlier state of existence, *when the present exceptional or arrested structure was normal*. The simple brain of a microcephalous [person], in as far as it resembles that of an ape, may in this sense be said to offer a case of reversion." (Darwin, 1871, I:122, emphasis mine).

Although microcephaly is now known to be a clinically, phenotypically, and genetically heterogeneous condition in humans, microcephalics nevertheless typically share certain shape features that distinguish them from normal humans. They usually have abnormally small skulls with sloping foreheads, and small brains that are narrow and flattened underneath in front, but with disproportionately large and protruding cerebella in back (Falk et al., 2007). Based on comparative molecular data, geneticists hypothesize that the *normal* variants of two of the genes (ASPM, MCPH5) that cause microcephaly when they are mutated were under strong positive selection related to the increase in brain size during hominin evolution (Evans et al., 2004; Gilbert et al., 2005). Others have questioned this finding, and suggested that ASPM (but not MCPH5) and another microcephalic gene, CDK5RAP2, were important for brain size evolution across higher primates in general, and not just in hominins (Montgomery et al., 2011). Findings from a comparative study of brain shape in microcephalics, normal humans, and fossil hominins are consistent with the hypothesis that normal variants of some of the genes associated with microcephaly may have been important during hominin brain shape (as well as size) evolution (Falk et al., 2007, 2009). Specifically, the typical pathological shape of the brains of modern microcephalics resembles the normal but primitive brain shape (and size) in a genus of fossil hominin (*Paranthropus*) that, at some point, separated form the hominin lineage that gave rise to *Homo*. These converging genetic and paleoneurological data fit with Darwin's notions about reversion in microcephalics, and I suspect that future comparative studies of mutated alleles that are associated with pathologies will provide additional windows for formulating hypotheses about hominin evolution. If so, Darwin was ahead of his time on reversions.

Darwin's classification of humans

Darwin meticulously compared traits of people with those of other animals, which led him to affirm Carl Linnaeus's earlier placement of humans in the order Primates (1871, I:190), and to conclude that, within the order's hierarchical classification, humans were closer to Old World than to New World monkeys (1871, I:196), and closer, still, to apes (1871, I:197). This is why Darwin hypothesized that humans arose from an ancient ape ancestor. At narrower taxonomic levels, Darwin speculated that humans comprised a family or sub-family within primates. He also considered the thorny question of whether the enormous geographical range and physical variation of humans warranted placing different populations in different species, as some advocated. However, after observing that the physical differences that separated human populations graduated into each other geographically (clinal variation) and that people from distinctly different groups "mingled" or "fused" (interbred) when their paths crossed (a biological definition of species), Darwin correctly concluded that all humans belong to one species, which he identified simply as "man." Curiously, he seems to have avoided referring to this species

as *Homo sapiens*, the formal name which Linnaeus had bestowed over a century earlier. Because Darwin's failure to refer to the binomial nomenclature for a species was so out of character, yet pervasive in his discussions about humans, it appears that he may have deliberately refrained from identifying humans as "*Homo sapiens*" for some, as yet, unknown reason.

Despite the fact that Darwin recognized the similarities shared worldwide by humans, he observed that geographically separated groups were variable to a degree that, in other animals, would warrant classifying them into different subspecies. For humans, however, Darwin preferred to describe such groups as races rather than subspecies. [He could not have anticipated how politically-incorrect the term "race" would become, at least among today's anthropologists (Brace, 2005), when he wrote that, for humans, "from long habit the term 'race' will perhaps always be employed" (1871, I:227-228).] Darwin noted that "various races, when carefully compared and measured, differ much…as in the texture of the hair, the relative proportions of all parts of the body, the capacity of the lungs,….also in constitution, in acclimatization, and in liability to certain diseases" (1871, I:216). He attempted to determine the causes of racial variation, and concluded that environmental conditions, inheritance of acquired traits, inheritance of correlated traits, and natural selection "cannot be of much importance….We have thus far been baffled in all our attempts to account for the differences between the races of man" (1871, I:249). [As an aside, Darwin's analysis was based partly on questionable assumptions. For example, having remarked that skin color was the most conspicuous difference between races, he argued that it had little to do with climate and geographical latitude (Darwin, 1871, I:241, 245-246), which is now known to be incorrect (Jablonski, 2006).]

Darwin then proposed that another important evolutionary agency that acts on animals, namely sexual selection, accounted significantly for the differences between human races. The classic example of sexual selection is the peacock, in which the tail feathers of males became elaborated during evolution because peahens preferred to mate with (and, therefore, propagate the genes of) individuals that performed courtship displays with relatively extravagant tails. Their gorgeous plumage, thus, represented a secondary sexual character that gave males a competitive advantage in obtaining mating opportunities (1871, I:258, 271), as opposed to the primary sexual characters that simply distinguish the reproductive organs of male and female animals (1871, I; 253). Less frequently, it is the females of a species that possess pronounced secondary sexual traits, and "in some cases a double process of selection has been carried on; the males having selected the more attractive females, and the latter the more attractive males" (1871, I:276). Darwin thought that humans were one such case, because of their high degree of differences between the sexes (sexual dimorphism) in a suite of features including stature, muscularity, body shape, amount and distribution of hair (including beards, whiskers, moustaches), voice, temperament, and perhaps "tint" (skin color) (1871, II:316-317). In fact, he opined that it would be "an inexplicable fact" if humans had not been modified

by sexual selection, and observed that [in other animals] the differences between human races such as "colour, hairyness, form of features, etc., are of the nature which it might have been expected would have been acted on by sexual selection" (1871, I:249-250).

Darwin referred to animal husbandry in developing his theory about the contribution of sexual selection to the evolution of human races (1871, II:369-370). He noted that an animal breed in which the most approved individuals are preserved changes after several generations, and that two independent breeders working from the same basic stock will, over time, end up with animals that differ because each breeder will have impressed "the character of his own mind—his own taste and judgment—on his animals" (1871, II:370). Darwin observed that conventions of beauty vary markedly from culture to culture in contemporary humans, and attributed this phenomenon to the gradual accumulation in the past of different unconscious preferences that resulted in different outcomes of sexual selection in geographically-separated groups. This short essay cannot do justice to the voluminous comparative data that Darwin amassed in developing his ideas about the relationship of sexual selection to the emergence of human races, so I will simply quote one of his many interesting examples: "It is well known that with many Hottentot [an earlier name for a Khoisan ethnic group from southwestern Africa] women the posterior part of the body projects in a wonderful manner; they are steatopygous; and…this peculiarity is greatly admired by the men" (1871, II:345-346). Unfortunately, Darwin's hypothesis about sexual selection and the development of racial differences is unlikely to receive the scrutiny it deserves as long as the term "race" is so negatively-loaded that (many) anthropologists shy away from studying the subject.

Although Darwin, by no means, attributed all of human racial variation to sexual selection, he made a strong case that this mechanism acted significantly on both men and women and, thus, contributed importantly to modifications that accumulated in widely-separated groups and therefore, eventually, facilitated their identifications as distinct races. On the other hand, Darwin also pointed out that, because of the similarities shared by people everywhere, humanity was descended from one common ancestor, i.e., he was a monogenist. A man of his times, Darwin was prone to making value judgments that had racist (and sexist) overtones that were acceptable within his cultural circles in Victorian England, but sometimes tempered them in light of his personal observations. For example, "I was continually struck with surprise how closely the three natives [Fuegians] on board H.M.S. 'Beagle,' who had lived some years in England and could talk a little English, resembled us in deposition and in most of our mental faculties" (1871, I:34). Elsewhere, Darwin noted that the similarities of ancient stone tools from different parts of the world could only be accounted for by the various races sharing similar mental and inventive abilities (1871, I:233).

Darwin's hypotheses about early human ancestors

Vertebrate morphology, embryology, and the study of anatomical rudiments and reversions mentioned above provided the foundations for Darwin's conjectures about early hominins. He envisioned extremely ancient monkeylike ancestors of humans as "no doubt once covered with hair, both sexes having beards; their ears were pointed and capable of movement; and their bodies were provided with a tail....The foot, judging from the condition of the great toe in the foetus, was then prehensile; and our progenitors, no doubt, were arboreal in their habits, frequenting some warm, forest-clad land. The males were provided with great canine teeth, which served them as formidable weapons" (1871, I:206-207). Darwin speculated that more recent ancestors diverged from monkeylike stock and evolved into a form similar to the African apes (chimpanzees and gorillas), which he correctly recognized as the closest living relatives of humans (1871, I:199). He therefore inferred that tropical Africa may have been the cradle of humanity, where early apelike progenitors lost their tails, and became divested of most (but not all) hair because of exposure to heat in conjunction with sexual selection that affected distribution patterns and degrees of hairiness "for ornamental purposes" (1871, I:149).

Darwin realized that, among living primates, habitual bipedalism had evolved only in the human lineage, which resulted in freed forelimbs that were modified for prehensile activities including the manufacture and use of tools, defense, and obtaining food. The evolution of bipedalism, he opined, had been progressive and associated with endless changes throughout the body (1871, I:143). In this context, and without benefit of the hominin fossil record that would eventually be discovered, Darwin hypothesized that the relatively large canines and jaws of males became reduced over time as our progenitors gradually came to depend more on use of stones, clubs and other weapons.

Although proponents of punctuated equilibrium (Eldredge & Gould, 1972) suggest that Darwin mistakenly believed that evolution was always a slow, continuous process, he knew that the rate at which populations evolved could increase greatly under some circumstances: With respect to "how rapid a rate organisms…may under favorable circumstances be modified,….within the same period some…co-descendants of the same species may be not at all changed, some a little, and some greatly changed. Thus it may have been with man" (Darwin, 1871, I:200). Nor was Darwin the least bit troubled by the "absence of fossil remains, serving to connect man with his ape-like progenitors" (1871, I:201). The discovery of all vertebrate fossils was extremely slow and fortuitous, he reasoned, and the right parts of the world for finding remains of our ancestors had not yet been searched by geologists. Gaps in the animal fossil record also did not bother Darwin, which he attributed to the number of related forms that had become extinct. He also explained the huge differences between living forms such as humans and apes with similar reasoning, and predicted that living great apes would soon become extinct, rendering the gap between humans and other living primates even wider. Darwin expected fossils to be discovered that would confirm his hypotheses about human evolution, and eventually they were.

The evolution of human cognition fascinated Darwin. "No one," he wrote, "supposes that one of the lower animals reflects whence he comes or whither he goes, —what is death or what is life, and so forth" (1871, I:62). He believed, however, that the differences between the mental (and moral) faculties of humans and other higher primates are ones of degree rather than kind (1871, I:34-35). To a surprising extent, Darwin's analyses of human mentality foreshadowed discussions of contemporary evolutionary psychologists. Thus, because of the "activity of [their] mental faculties," humans cannot avoid reflection (1871, I:89), and are impelled to experience the states of pain and pleasure observed in others (1871, I:81) (known today as possessing Theory of Mind). As documented in the Appendix, Darwin paved the way for modern discussions about the evolutionary significance of reciprocal altruism, group selection, and social intelligence.

Darwin was struck by the fact that "articulate language" is peculiar to humans (1871, I:54), and speculated that language evolved incrementally and gradually from primate vocalizations. In so doing, he advocated a *continuity hypothesis* rather than the opposing *discontinuity hypothesis*, held by some scholars today, that language appeared suddenly, without phylogenetic links to earlier communication systems (see Falk, 2004, 2009 for details). Referring to gibbon song (1871, I:56; II:332), Darwin argued that speech developed from musical notes and rhythms that had evolved in our progenitors "for the sake of charming the opposite sex" (1871, II:336). He envisioned the eventual emergence of a protolanguage "far less perfect than any now spoken, aided by gestures…[that] left no traces on subsequent and more highly-developed tongues" (1871, I:235).

Darwin theorized that there had been a feedback relationship between "the continued use of language and the development of the brain…The mental powers in some early progenitor of man must have been more highly developed than in any existing ape, before even the most imperfect form of speech could have come into use; but we may confidently believe that the continued use and advancement of this power would have reacted on the mind by enabling and encouraging it to carry on long trains of thought" (1871, I:57). Humans became the most dominant animals that ever appeared on earth, according to Darwin, because of their powerful intellects that facilitated the evolution of articulate language (1871, I:137). Interestingly, he considered the art of making fire the second greatest achievement of humanity.

Summary and conclusions

Despite the fact that he did not know what a gene was, and that the first fossil australopithecine would not be discovered until over four decades after his death (Dart, 1925), many of Darwin's hypotheses about human evolution were prescient. Surprisingly, his acceptance of Lamarck's idea that acquired characters could influence future generations foreshadowed today's emerging field of epigenetics. Consistent with some of Darwin's ideas about atavisms, comparative molecular studies of human pathologies, such as mi-

crocephaly, are just beginning to identify genes that may have been targets of positive natural selection during hominin evolution. Darwin also classified humans accurately at most levels within the Primate order, including his recognition that all people belong to one species ("man"), although, as far as I can tell, he did not formally attribute the species to *Homo sapiens*. In my view, he made a convincing argument that sexual selection operated significantly during human evolution, and that it probably had an impact on the emergence of racial variation. (Darwin, however, failed to appreciate the extent to which natural selection contributed to the emergence of human variation.)

He was even better on the not-yet-discovered hominin fossil record. His hypothesis that hominins originated in Africa turned out to be correct, as did his prediction that fossils of our earliest ancestors would eventually turn up in tropical habitats. Darwin accurately anticipated that "connecting-links [that] have not hitherto been discovered" (1871, I:185) between apes and humans would appear intermediary in the forms of their teeth, jaws, skulls, and bodies, to varying degrees depending on circumstances. He discussed the shift from arboreal to terrestrial locomotion in our ancestors, and understood the significance of bipedalism for human origins and cognitive evolution. Bipedalism, he argued, evolved gradually and affected the whole body. (The rate at which bipedalism evolved is a controversial subject today, but I think Darwin got it right.) Darwin's discussions about human social evolution were based on a thorough knowledge of ethnology, and he incorporated many of the concepts used by today's evolutionary psychologists into his thinking. Since at least Darwin's time, the topic of language origins has aroused strong and polarized opinions. His views that language originated from musical primate vocalizations and subsequently evolved into protolanguage and, eventually, full-blown language(s) were well reasoned and supported by comparative data (Falk, 2009).

Darwin referred to the evolution of "Man, the wonder and glory of the Universe" (1871, I:213). To modern ears, this smacks of the discredited idea that evolution made a predestined, or even supranatural, beeline toward the emergence of humans (orthogenesis). This is not what Darwin meant, however, and he shall have the last word here to explain himself: "The world, it has often been remarked, appears as if it had long been preparing for the advent of man; and this, in one sense is strictly true, for he owes his birth to a long line of progenitors. If any single link in this chain had never existed, man would not have been exactly what he now is. Unless we willfully close our eyes, we may, with our present knowledge, approximately recognize our parentage; nor need we feel ashamed of it" (Darwin, 1871, I:213).

Appendix

Concepts recognized by Charles Darwin, quoted from *The Descent of Man*, Volume I, 1871 (unless otherwise stated). Quotations are followed by contemporary terms for the concepts in parentheses.

p. 16 "The embryo of man closely resembles that of other mammals…[it] resembles in various points of structure certain low forms when adult….Even at a later embryonic period, some striking resemblances between man and the lower animals may be observed." (evo-devo)

p. 18 "Rudimentary organs are eminently variable; and this is partly intelligible, as they are useless … and consequently are no longer subjected to natural selection" (natural selection narrows a trait's range of variation)

p. 82, "mankind…led by the hope of receiving good in return to perform acts of sympathetic kindness to others" (reciprocal altruism)

also see p. 163, "As the reasoning powers and foresight of [a tribes's] members became improved, each man would soon learn from experience that if he aided his fellow-men, he would commonly receive aid in return."

p. 82, "as it [reciprocal altruism] is one of high importance to all those animals which aid and defend each other, it will have been increased, through natural selection; for those communities, which included the greatest number of the most sympathetic members, would flourish best and rear the greatest number of offspring" (group selection)

also see p. 155, "With strictly social animals, natural selection sometimes acts indirectly on the individual, through the preservation of variations which are beneficial only to the community…although each separate member may gain no advantage over the other members of the same community" (group selection)

p. 114, "…changed conditions induce an almost indefinite amount of fluctuating variability, by which the whole organization is rendered in some degree plastic" (environmental effects)

p. 120, "residence [of humans]…at a great elevation tends…to induce inherited modifications in the proportions of the body" (high-altitude adaptation)

p. 122, "the simple brain of a microcephalous idiot, in as far as it resembles that of an ape, may in this sense be said to offer a case of reversion" (atavisms or evolutionary throwbacks)

p. 130, "many structures are so intimately related, that when one part varies so does another, without our being able, in most cases, to assign any reason" (pleiotropy)

p. 136, "law of natural selection…Beneficial variations…will thus…have been preserved, and injurious ones eliminated. I do not refer to strongly-marked deviations of structure, which occur only at long intervals of time, but to mere individual differences" (macro versus micro evolution)

p. 152, “Modifications acquired and continually used during past ages…would probably become firmly fixed and might be long inherited” (fixation of traits)

p. 152, “in the earlier editions of my ‘Origin of species’ I probably attributed too much to …natural selection….I had not formerly sufficiently considered the existence of many structures which appear to be…neither beneficial nor injurious” (evolutionarily neutral traits)

p. 152-3, “natural selection had been the chief agent of change, though largely aided by the inherited effects of habit, and slightly by the direct action of the surrounding conditions” (Lamarckian inheritance & influence of environmental factors)

153-4, “Uniformity of character would, however, naturally follow from …the free intercrossing of many individuals’ (gene flow)

p. 153-4, Regarding “modifications …kept uniform through natural selection”… “the[ir] existing causes…, as when speaking of so-called spontaneous variations…relate much more closely to the constitution of the varying organism, than to the nature of the conditions to which it has been subjected” (genes and mutations)

p. 160, “As soon as the progenitors of man became social…the advancement of the intellectual faculties will have been aided and modified in an important manner” (social intelligence hypothesis)

p. 161, “Even if [superior and inventive men] left no children, the tribe would still include their blood-relations; and it has been ascertained by agriculturists that by preserving and breeding from the family, the desired character has been obtained” (kin selection)

p. 188, “the co-descendants of the same form must be kept together in one group, separate from the co-descendants of any other form…. We have no record of the lines of descent, these lines can be discovered only by observing the degrees of resemblance between the beings which are to be classed… numerous points of resemblance are of much more importance than the amount of similarity…in a few points….The points of resemblance must not consist of adaptations to similar habits of life” (foreshadows cladistic analysis)

also see p. 211, “as organisms have become slowly adapted by means of natural selection for diversified lines of life, their parts will have become…more and more differentiated and *specialized* for various functions.” (emphasis mine)

p. 194, “It must not be supposed that the resemblances…are all necessarily the result of unbroken inheritance from a common progenitor…Many of these resemblances are more probably due to analogous variation, which follows…from co-descended organisms having a similar constitution and having been acted on by similar causes inducing variability” (parallel evolution)

p. 199, “we must not fall into the error of supposing that the early progenitor of…man was identical with, or even closely resembled, any existing ape or monkey” (branching evolution)

p. 211, “The same part appears often to have been modified first for one purpose, and then long afterwards for some other and quite distinct purpose” (exaptation)

also see pp. 331 and 335 of Vol II re exaptations of apparatus for inhaling and expelling air in vertebrates for courtship purposes

p. 212, In "Vertebrata…groups of organic beings are always supplanted and disappear as soon as they have given birth to other and more perfect groups….Some old forms appear to have survived from inhabiting protected sites" (extinctions)

also see p. 238, "Extinction [in humans] follows chiefly from the competition of tribe with tribe, and race with race."

p. 226, "the races of man…graduate into each other, independently in many cases,…of their having intercrossed"…."it is hardly possible to discover clear distinctive characters between them" (clines)

p. 236, "the horses which have been brought to the Falkland Islands have become, during successive generations, smaller and weaker, whilst those which have run wild on the Pampas have acquired larger and coarser heads" (island effect)

p. 262, "In a multitude of cases the males which conquer other males, do not obtain possession of the females, independently of choice on the part of the latter" (female choice)

p. 278-9, Regarding "the frequent and extraordinary amount of variability presented by secondary sexual characters,….development…of the horns, for instance, in certain stags—has been carried to a wonderful extreme; and in some instances…must be slightly injurious to the male" (runaway [Fisherian] sexual selection)

p. 282, "But characters are not rarely transferred exclusively to that sex, in which they first appeared" (sex-linked traits)

p. 297-8, "If … a certain proportion of the offspring …vary…in some manner which…was of no service to them, the chance of the preservation of such variations would be small. We have good evidence under domestication how soon variations of all kinds are lost, if not selected." (basis of probable mutation effect [PME])

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