Descended from Darwin

Insights into the History of Evolutionary Studies, 1900–1970

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Chapter 5

Descended From Darwin?

George Gaylord Simpson, Morris Goodman, and Primate Systematics

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Introduction

In 1962 the immunologist Morris Goodman unwittingly ignited a controversy when he reported that experiments based on antibody-antigen reactions showed no detectable differences in serum proteins drawn from humans, gorillas, and chimpanzees (Goodman, 1962). Based upon these results, he proposed that all three primates should be united within the family Hominidae. The biochemist Emile Zuckerkandl caused a greater stir at the same meeting by claiming that humans and gorillas were members of the same "population."[1] Proclaiming the birth of a new discipline of "molecular anthropology," Zuckerkandl pointed out that peptide fingerprints of gorilla, chimpanzee, and human hemoglobins were indistinguishable.[2] The sequences of amino acids in the α and β polypeptides of hemoglobin were not completely known at the time, but evidence indicated that humans and gorillas might differ by only a single amino acid in the β chain and one, or perhaps two, amino acids in the α chain. According to Zuckerkandl, gorilla β hemoglobin was likely no more different from normal human hemoglobin than the hemoglobin of patients with sickle cell anemia. "Therefore," he claimed, "from the point of view of hemoglobin structure, it appears that gorilla is just an abnormal human, or man an abnormal gorilla, and the two species form actually one continuous population."[3] As a result of rare mutations, Zuckerkandl claimed it was probable that some living humans carried gorilla hemoglobin and vice versa.

Goodman and Zuckerkandl presented their papers at a conference on human evolution and classification sponsored by the Wenner-Gren Foundation at Burg Wartenstein, near Vienna, Austria. Among those in attendance were the distinguished evolutionary biologists George Gaylord Simpson, Ernst Mayr, and Theodosius Dobzhansky. Simpson brushed aside Zuckerkandl's claim about the closeness of the relationship between humans and gorillas: "From any point of view other than that properly specified [hemoglobin structure], that is of course nonsense. What the comparison seems really to indicate is that in this case, at least, hemoglobin is a bad choice and has nothing to tell us about affinities, or indeed tells us a lie."[4] In the published version of his conference paper, Simpson leveled several counterarguments against Goodman's proposed change in primate classification, which he characterized as "radical."[5] He strongly reaffirmed his long-held position placing apes and humans into two separate families: Pongidae (chimpanzees, gorillas, orangutans, and gibbons) and Hominidae (humans).

Both Zuckerkandl and Goodman later recalled having their ideas rebuffed by the leaders of evolutionary synthesis.[6] According to Zuckerkandl, Simpson had an "allergic reaction" to molecular evolutionists—a characterization amplified by a number of recent historical studies.[7] Goodman expressed surprise at Simpson's rejection of his ideas, and he characterized the events at Burg Wartenstein as the beginning of a paradigm shift in primate studies. Accusing Simpson of being overly metaphysical, anthropocentric, and pre-Darwinian in his taxonomy, Goodman later portrayed his own early immunological studies as important steps in establishing a purely cladistic classification of the primates and for documenting the very close evolutionary relationships among humans, chimpanzees, and gorillas (Goodman, 1996).

With hindsight Goodman's historical account is plausible. Later research convincingly demonstrated that humans, chimps, and gorillas are genetically very similar—perhaps even more so than Zuckerkandl or Goodman could have imagined in 1962 (e.g., Wildman, Uddin, Liu, Grossman, & Goodman, 2003). Most taxonomists today reject the theoretical basis of Simpson's approach to evolutionary systematics and important elements of his classification of primates. In that sense, too, Goodman's early revision of primate classification appears prescient. Still, the story leaves largely unexamined the ways in which Goodman initially worked within the intellectual framework provided by Simpson's contributions to the evolutionary synthesis and its sibling the new systematics (later called evolutionary systematics). It distorts and obscures Simpson's important role in the development of primate studies after World War II, his complex views on human nature, and his conflicted attitudes toward newer ideas impinging on evolutionary systematics near the end of his career. Both Simpson and Goodman considered themselves intellectual descendants of Darwin. Initially, Goodman included Simpson as an important member of his own Darwinian heritage. Intriguingly, he later denied that Simpson was part of that intellectual lineage. A more detailed comparison of the views of Goodman and Simpson thus provides a useful perspective for examining the shifting influence of the evolutionary synthesis on primate phylogeny and classification.

Background to the Controversy: Goodman's Immunodiffusion Studies

At Burg Wartenstein, Goodman was a relative newcomer to the fields of primate evolution and classification. Beginning in the late 1950s, he used gel electrophoresis and immunodiffusion experiments to compare blood serum proteins from various primates. The immunodiffusion technique, his main tool for studying primate relationships, was based upon reactions between specific antibodies and antigens. Antiserum (containing antibodies) was prepared by injecting serum from a primate species into another animal, usually a chicken or rabbit. The chicken or rabbit would then produce antibodies to the foreign protein (i.e., the antigen). These antibodies could later be harvested from the chicken's or rabbit's blood. Goodman's experimental apparatus, the Ouchterlony plate (Figure 5.1), was a T-shaped diffusion chamber with three reservoirs for serum connected by a slab of agar through which the sera diffused.

One reservoir contained the antiserum (containing the antibodies), and the other two wells contained primate sera (containing the proteins that acted as antigens) from the species that were being compared. When the diffusing antibodies and antigens met, they combined to form a visible precipitate. The pattern of precipitation gave a qualitative indication of the similarity of the two homologous proteins and less directly of the genetic similarity between the species. Obtaining serum from zoos and other research facilities, Goodman amassed a network of pair-wise comparisons among most of the major groups of primates, eventually involving some 5,600 experiments.[8]

Goodman introduced an important technical innovation allowing rapid and readily reproducible experimental results, but his plates were also part of a long and well-established tradition in systematic serology.[9] Beginning in the early years of the twentieth century, George Nuttall experimented with immunological techniques for

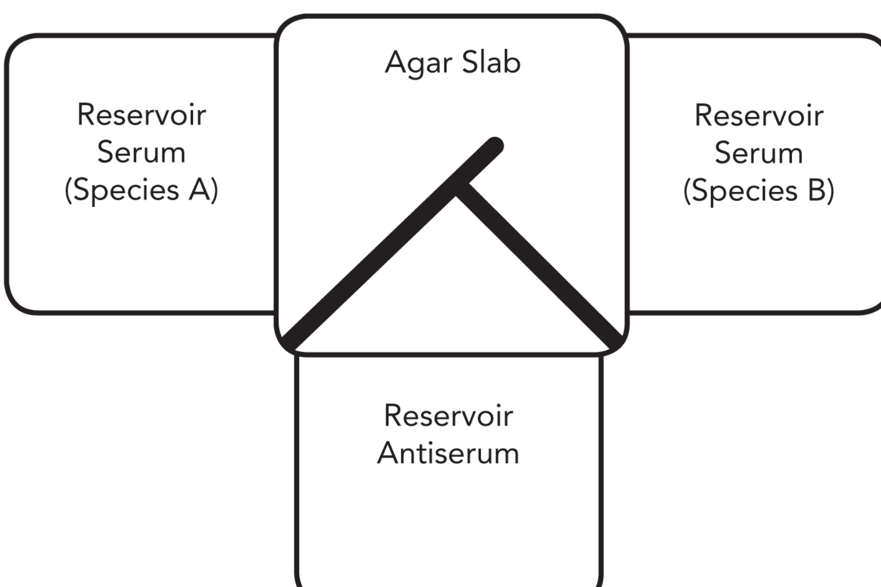

Figure 5.1. Diagrammatic representation of the Ouchterlony plate used in Goodman's immunological experiments. The bottom reservoir contains antibodies formed against a serum protein from Species A. The reservoir on the left contains this protein from Species A. The reservoir on the right contains the homologous serum protein from Species B. The sera and antiserum diffuse through the agar slab. Where they meet and react, a visible precipitate forms (black lines). The short "spur" on the line to the left represents antigens on the protein from Species A that are not present on the homologous protein from Species B.

comparing proteins from various mammals, including primates. The so-called "precipitin reaction" was later used by several biologists who were interested in systematics. This and other serological methods were widely accepted as useful additions to more traditional taxonomic procedures because they were relatively cheap and easy to perform and because they gave repeatable results. Established specialists in the field, such as Alan Boyden at Rutgers University, believed that they were making an important, if limited, contribution to classification. Referring to his own work, Boyden wrote, "Note that we have spoken of aiding systematists and not of producing definitive classifications based on serology alone. We feel that the most useful classification should be based on as broad and objective bases of study as possible; for the more we know of the nature of organisms, as we find them, the more biologically significant our taxonomy will become."[10] Boyden, perhaps the leading comparative serologist in the United States, was a friend of Simpson and carried on a long correspondence with him. When Goodman began studying comparative serology at the University of Wisconsin after World War II, he was trained by Harold Wolfe, one of Boyden's students. Goodman recalled working within the general framework of Boyden's serology and Simpson's new systematics, but by 1962 he disagreed with the two older biologists in at least one important way. Because proteins were so closely related to genes, Goodman believed that they had a privileged status among taxonomic characters.[11]

Background to the Controversy: Simpson's Role in Primate Systematics

It is not surprising that serologists, particularly those interested in mammalian systematics, should have consulted Simpson about their research.[12] During the 1950s and 1960s, Simpson was at the height of his scientific influence, though not of his scientific creativity. His career can be conveniently divided into two parts by World War II. Most of Simpson's original scientific research was completed by the time that he entered the army in December 1942. Just before he enlisted, Simpson finished two major works: the highly theoretical *Tempo and Mode in Evolution* (Simpson, 1944) and an important taxonomic monograph, *The Principles of Classification and a Classification of the Mammals* (Simpson, 1945). These, together with his earlier technical papers in mammalian paleontology, established him as a leading figure in evolutionary biology and mammalian systematics.

Tempo and Mode was a cornerstone of the evolutionary synthesis. In the book, Simpson forcefully argued for the central role of paleontology in evolutionary studies (Cain, 1992, 2003; Laporte, 2000). As a uniquely historical science, it provided both the evidence for evolutionary change and ways of thinking that complemented, but could not be replaced by, experimental sciences such as genetics (Simpson, 1944, p. xvii). This argument for interdisciplinary cooperation was a central part of Simpson's view of the evolutionary synthesis, and it showed up repeatedly in his later writings. *Tempo and Mode* also discredited older evolutionary ideas like orthogenesis and saltation. Simpson convincingly argued that macroevolutionary phenomena studied by paleontologists could be explained by the microevolutionary mechanisms of population genetics. He also provided a novel theoretical basis for understanding evolutionary rates. His idea of quantum evolution, when a population evolves rapidly into a previously unoccupied adaptive zone, played a key role in his interpretation of evolutionary patterns in the primates and the taxonomic relationships among humans and apes.

Simpson's later views on primate evolution were particularly influential. He was perhaps the leading expert on the taxonomy of mammals, both living and extinct. His 1945 revision of mammal classification remained a definitive reference work for several decades. The book fell within the tradition of museum taxonomy, but Simpson also included a long chapter on taxonomic principles that was an early statement of the new systematics. Two themes emerged from the chapter. First, the new systematics was interdisciplinary, requiring methods and evidence from many fields. Second, classification had to be consistent with what was known of phylogenetic history, although it could not usually be based strictly on phylogenetic relationships. By emphasizing these two points, he once again argued for the unique role of paleontology in the broader interdisciplinary fields of evolutionary biology and evolutionary systematics (Cain, 1992).

Simpson later expanded these ideas in his *Principles of Animal Taxonomy* (1961), perhaps the most detailed and influential statement of the mature evolutionary systematics that had grown out of the earlier new systematics. Although less active in field and museum research than he had been before World War II, Simpson continued to maintain an enthusiastic interest in studying primate fossils during this later period. In particular, a visit to Louis and Mary Leakey's research site near Olduvai Gorge in 1961 apparently made a deep impression on Simpson's thinking about human evolution (Simpson, 1978, chap. 19).

During the decades following World War II Simpson consolidated his influence by writing semipopular books and articles aimed at an expanding audience made up of scientists in other disciplines, students, and the general public. These writings also provided the opportunity to explore the philosophical implications of his earlier works, particularly as applied to human nature. Simpson also became an important discipline builder, holding offices in several professional organizations dealing with mammalogy, taxonomy, and evolutionary biology (Laporte, 2000, pp. 11–12, 40). By the time Goodman met him in 1962, Simpson was an imposing senior scientist and an intellectual authority to be reckoned with.

Scientists and historians have characterized this later period of Simpson's career in a variety of ways. Portraying him as an increasingly conservative thinker, Stephen Jay Gould described how Simpson contributed to the "hardening of the synthesis" (Gould, 1995). According to Gould, Simpson missed the opportunity to creatively expand on his earlier discussions of evolutionary rates. Instead, Gould claimed, Simpson later downplayed quantum evolution and overemphasized evolutionary gradualism. Several other younger scientists also criticized Simpson for becoming a scientific reactionary who impeded progress in systematics and evolutionary studies.[13] In part, Goodman's critique of Simpson can be viewed as another example of this generational shift in scientific authority.

Joe Cain has described how Simpson's career can be viewed from the perspective of his strongly held view that the evolutionary synthesis was an interdisciplinary enterprise that required cooperation among various disciplines, each making its own unique contribution (Cain, 1992, 2003). However, in practice, there was a real tension between this view that Simpson had long espoused and the realities of incorporating the new approaches to evolution championed by younger scientists like Goodman. This tension was particularly pronounced during the 1960s, when Simpson was nearing the end of his career. Several historians have explored Simpson's role in what he sometimes referred to as a "clarifying confrontation" with molecular evolution, new schools of taxonomy, and new quantitative methods in systematics. Dietrich (1998) has characterized Simpson's efforts in these episodes as a form of negotiation over the boundaries of various fields in evolutionary biology. In a much more sympathetic account, Laporte (2000, chap. 8) has portrayed the older Simpson as a "mentor" who brought modern evolutionary thinking to disciplines like physical anthropology, which had not taken part in the evolutionary synthesis. Even Laporte acknowledges, however, that by the 1960s newer approaches to studying primates were encroaching upon Simpson's more established views.

According to Laporte, Simpson's mentoring took a number of forms. In some cases, those interested in primate evolution turned directly to Simpson's earlier, more technical works. But probably more often the ideas were received second hand. Simpson summarized his main ideas prominently in a number of conference presentations. These presentations tended to be broad overviews that criticized earlier theories of human evolution and showed how the synthetic theory could better explain the fossil record and comparative anatomy of primates. Many anthropologists also learned about evolutionary biology from reading Simpson's semipopular books, most notably *The Meaning of Evolution* (1949), subtitled *A Study of the History of Life and of Its Significance for Man*. This book was widely used as a textbook in introductory anthropology courses. It sold over half a million copies and was translated into several languages. It also influenced later anthropology textbooks, notably W. Le Gros Clark's (1959) *The Antecedents of Man*. Clark's book adopted Simpson's system of primate classification, and it presented numerous examples and illustrations drawn from *The Meaning of Evolution*.

In a general way, Laporte's idea of mentoring might also be applied to Goodman's introduction to primate taxonomy and evolution, probably by reading Simpson's *The Meaning of Evolution*, and Le Gros Clark's *Antecedents of Man*, in about 1959. Goodman cited these books in his earliest papers on comparative serology. Shortly thereafter he immersed himself in Simpson's "Classification of Mammals" and *Principles of Animal Taxonomy*. He also corresponded with Simpson, describing the immunodiffusion experiments he was performing. When he gave his talk at Burg Warteinstein in 1962, Goodman believed that he was working within the broad taxonomic and evolutionary framework established by Simpson and Le Gros Clark.[14] From Goodman's point of view, placing gorillas, chimpanzees, and humans in the same family was an important improvement to—but not a radical break from—Simpson's overall approach to classification. Gradually as the controversy continued, Goodman rejected several other aspects of Simpson's thinking. Looking back on his career in the 1990s, Goodman argued that his initial proposition was just as "radical" as Simpson had initially claimed. Interestingly, however, that is not how Goodman saw the situation in 1962.

Diverging Views on Primate Classification

Simpson was highly critical of primate classification, which he described as a "mess" (Simpson, 1949, p. 81, and 1950). "The fossil record is none too good," he wrote, "inferior to that for most orders of mammals, and would hardly merit special attention here if it were not the record of our own order so that we are inclined to make the most of it" (Simpson, 1949, p. 84). Without adequate fossil evidence, dates of divergence were necessarily speculative and some evolutionary relationships were obscure. The problem of classification was compounded by the contentious issue of human origins and by the proliferation of scientific names, often proposed by anthropologists with little taxonomic training (Bowler, 1986). Despite misgivings, Simpson laid down the broad outline of his classification for the order in his 1945 monograph. His discussion reflected a concern for phylogenetic relationships, but also traditional taxonomic issues of nomenclature, priority, lumping versus splitting, stability, and general usefulness (Simpson, 1945, pp. 180–189). Indeed, a key consideration in Simpson's evolutionary systematics was finding an acceptable balance among these conflicting demands.

Within the order primates, Simpson recognized four major structural types or "grades": prosimians, monkeys, apes, and humans. Because of parallel evolution, these grades did not necessarily correspond to monophyletic lineages or clades. The prosimians (a suborder) included a diverse group of lemurs, tarsiers, and perhaps tree shrews. Various prosimian groups represented the termini of ancient lineages that had little in common other than that they were not anthropoids (the other suborder of primates). The anthropoids were made up of humans, apes, and two quite distinct groups of monkeys. Simpson believed that old- and new-world monkeys had evolved independently from two ancient prosimian-like ancestors. They shared certain monkey characteristics as a result of convergent evolution. In this case, clades were more important than grades, and Simpson separated the old- and new-world monkeys into two distinct superfamilies. The other superfamily, Hominiodea, included the gibbons, orangutans, chimpanzees, gorillas, and humans. This superfamily was divided into family Pongidae (the apes) and family Hominidae (humans), each representing a distinct evolutionary grade. In this case grades were more important than clades, because Simpson was willing to separate hominids from pongids, even though he acknowledged that they formed a single "natural unit" (Simpson, 1945, pp. 187–188).

In separating pongids and hominids, Simpson was breaking with his own mentor, William King Gregory, who recognized only one family. In justifying his position, Simpson explained, "On the basis of usual diagnostic characters, such as the teeth, viewed with complete objectivity, this union seems warranted. I nevertheless reject it, for two reasons: (a) mentality is also a zoological character to be weighed in classification and evidently entitling man to some distinction, without leaning over backward to minimize our own importance, and (b) there is not the slightest chance that zoologists and teachers generally, however convinced of man's consanguinity with the apes, will agree on the didactic or practical use of one family embracing both" (Simpson, 1945, pp. 187–188).

Anthropocentrism aside, Simpson's classification of primates illustrates a number of characteristics of evolutionary systematics that would become controversial and widely rejected by later systematists. For Simpson, classification was a balancing act involving an assessment of degrees of resemblance, probable phylogenetic relationships, and the practical needs of biologists who depended on a stable and easy-to-use system (Simpson, 1962, p. 25). Phylogeny was important to Simpson, but he was skeptical about granting too much validity to phylogenetic reconstructions, particularly in cases such as the primates where the fossil record was so incomplete. He also claimed, notoriously, that there was both an art and a science to such reconstructions involving a fair amount of subjective judgment. In reconstructing phylogeny, Simpson argued for using all available characteristics, both ancestral and derived, although certain characteristics might be more heavily weighted than others. Thus, he justified separating apes from humans partly on the basis that the pongids represented conservative lineages that retained many ancestral characteristics. Though clearly related to these ancestral traits, distinctive human characteristics including habitual bipedalism, advanced tool making (i.e., using tools to make other tools), and highly developed language warranted the recognition of a separate evolutionary grade.

Simpson's notion of evolutionary grades was closely tied to his ideas of tempos and modes in evolution. Quantum evolution involved an adaptive radiation of a lineage into a previously unoccupied ecological zone. In some cases, notably *Homo sapiens*, such a shift justified separating a taxon from its closest relatives. The idea of grades does not necessarily involve belief in a hierarchy of higher and lower. On this issue Simpson was inconsistent, both in his discussions of phylogeny and in the illustrations that accompanied them (Figure 5.2).

Sometimes he discussed grades in the neutral language of adaptation to particular circumstances, with taxa representing the tips of branches on a bushy evolutionary tree. At other times, however, he argued that not only were humans unique hominoids but also they were at a higher evolutionary level than other primates. Simpson's ideas of quantum evolution, evolutionary grades, and human uniqueness were not idiosyncratic. Other leading vertebrate taxonomists and evolutionary biologists shared these views. For example, in rebutting Zuckerkandl's claims about the close similarity of humans and gorillas, Mayr argued that humans had evolved at a rate almost unprecedented in evolutionary history: "If you would draw a phylogenetic tree on the blackboard, the human line would shoot off in a totally different new direction almost parallel to the base line. The resulting taxon is something quite novel in the history of the organic world."[15]

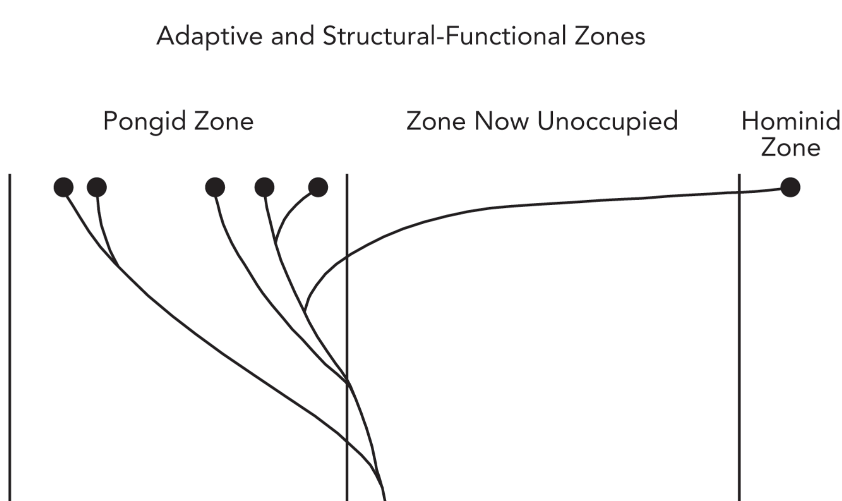

Figure 5.2. Simpson justified separating humans from apes on the basis of quantum evolution. The lineage leading to modern humans had entered a new adaptive zone or evolutionary grade. Note that in this diagram Simpson does not represent the hominid grade as higher than the pongid grade.

Simpson's belief in human uniqueness was evident in his 1945 monograph, but he refined this idea after World War II. In 1947 Simpson was invited to give the Vanuxem lecture at Princeton University and in 1948 the Terry lectures at Yale. Both of these endowed lecture series had been established to discuss science in a broad philosophical context and to explore the implications of science for religion. Simpson had rejected formal religion when he was a teenager (Laporte, 2000, pp. 70–72). However, as a paleontologist who struggled to establish a historical biology that could not be reduced to laws of physics, he was also philosophically opposed to reductionism. Like other leading spokesmen for the synthesis, Simpson advocated a form of evolutionary humanism that struck a balance between mechanistic materialism and purposive progressionism (Smocovitis, 1996, chap. 5). His views were, on the one hand, strongly selectionist and adaptationist but, on the other, deeply humanistic. Simpson criticized what he considered to be extreme views on these issues, and he formulated his own delicate balance, viewing humans both as a product of evolution and also something "new under the sun" (Simpson, 1947, p. 481). The Terry lectures provided the outline for Simpson's most popular book, *The Meaning of Evolution*, in which he explored these ideas in considerable detail.

The idea of evolutionary progress was particularly problematic for Simpson. Throughout his career Simpson criticized paleontologists who misused assumptions of progress and linear trends to interpret the fossil record. His *Tempo and Mode* had dealt a devastating blow against orthogenesis, aristogenesis, and other paleontological theories of progressive evolution. In his Vanuxem lecture, Simpson criticized the well-known physical anthropologist and philosopher Father Pierre Teilhard de Chardin, whose evolutionary progressivism he dismissed as metaphysical and unscientific. Simpson also distanced himself from the idea of overall evolutionary progress with humans as the endpoint. This view had been forcefully argued by Julian Huxley.[16] By contrast Simpson held a more pluralistic view of progress.[17] He denied progress had any meaning in biology unless criteria for measuring it were specified *a priori*. Progress was always relative to some point of reference, and even then it was prone to misuse.

This criticism of simple-minded anthropocentrism, was balanced by Simpson's equal disdain for biologists who rejected anthropocentrism out of hand:

> It is merely stupid for a man to apologize for being a man or to feel, as with a sense of original sin, that an anthropocentric viewpoint in science or in other fields of thought is automatically wrong. It is, however, even more stupid, and even more common among mankind, to assume that this the *only* criterion of progress and that it has a *general* validity in evolution and not merely a validity relative to one only among a multitude of possible points of reference. (Simpson, 1949, p. 242)

Anthropocentrism could be justified because humans are naturally inclined toward a human-centered understanding of the world. Birds, if they were intellectually capable, would likely develop their own avian-centered views of evolutionary progress.

Later in *The Meaning of Evolution* Simpson made a much stronger case for anthropocentrism. In the chapter "Man's Place in Nature," he argued not only that humans are unique but also that they are the highest form of animal life. Revisiting the image of avian intellectuals mentioned above, Simpson modified it to argue for a more thoroughgoing anthropocentrism. Humans were so different from all other animals, he argued, that if a fish could think it would be amazed that any human would question the proposition that *Homo sapiens* is the highest form of life. Of course, he added, if the fish could think in such an abstract way it would, in fact, have become a human. Humans' unique intellect allowed them not only to know that they are products of evolution but also to free themselves from many evolutionary constraints, to radically modify their environments, and perhaps to direct the future course of evolution. This power—not always used for good—also entailed a unique sense of responsibility, ethics, and values. "It is important to realize that man is an animal," Simpson wrote, "but it is even more important to realize that the essence of his unique nature lies precisely in those characteristics that are not shared with any other animal. His place in nature and its supreme significance to man are not defined by his animality but by his humanity" (Simpson, 1949, p. 284).

Simpson was sharply critical of unnamed biologists and philosophers who argued that humans are "nothing but animals" or that they were nothing but apes "with a few extra tricks." Such thinking was not only false; it was viciously misleading because it distorted human nature and undermined human values and ethics. Simpson's anthropocentrism sought a middle ground between the unacceptable view that humans were an inevitable product of evolution and the equally unacceptable view that they were merely an evolutionary accident. His views on human nature reinforced his decision to place humans in a separate family from their nearest primate relatives. It also was undoubtedly partly behind his "allergic reaction" to the taxonomic claims made by Zuckerkandl and Goodman about humans and apes at Burg Wartenstein.

Goodman's Revision of the Hominoidea

Goodman was not trained as a taxonomist, nor does it appear that he had read deeply in the literature of mammalian or primate taxonomy before he began his immunodiffusion studies. He began working within the general taxonomic framework presented by Simpson's semipopular book *The Meaning of Evolution* (1949) and repeated in W. E. Le Gros Clark's *The Antecedents of Man* (1959), which also presented a very general outline of Simpson's classification scheme for the primates.

Based on antigen-antibody reactions to serum albumin and some other blood proteins, Goodman found no detectable differences among gorillas, humans, and chimpanzees. The immunodiffusion patterns for all three of these primates diverged slightly from the orangutan, and further from the gibbon. These experimental results supported moving gorillas and chimpanzees from the family Pongidae to the family Hominidae. Goodman also favored removing gibbons from family Pongidae and placing them in a new family, Hylobatidae. The Pongidae now contained only the orangutans. From Goodman's perspective, the immunodiffusion data was particularly compelling because his proteins provided a close approximation of the actual genetic relationships among the primate species. His proposed revision also found independent support from Zuckerkandl's hemoglobin fingerprint analysis of humans and apes. Furthermore, Goodman argued that the revision was supported by morphological considerations, and he traced this line of reasoning back to Darwin's *Descent of Man*. Contrary to Simpson's claim that his revision was "radical," Goodman downplayed the break from traditional taxonomy based on morphological characters:

> Thus a systematics of the higher primates derived solely from serological data would not be much different from the established systematics which was largely derived from morphological data. A correspondence of the serological and morphological approaches is to be expected since the building blocks of morphological structures are proteins. (Goodman, 1962, p. 225)

Goodman was surprised at Simpson's vigorous criticism of his revision, because he was simply applying phylogenetic principles that he thought were accepted by Simpson, Mayr, and other evolutionary systematists. According to Goodman, "A broadening of the Hominidae to include *Gorilla* and *Pan* as well as *Homo* would reflect more closely the cladistic and genetic relationships suggested by the serological data" (Goodman, 1962, p. 225). This statement is important for a number of reasons. It reveals Goodman's early commitment to a purely phylogenetic classification based upon molecular characteristics. By omission, it also suggests that Goodman was not very concerned about other issues in museum taxonomy such as stability, simplicity, and usefulness that Simpson considered so important for classification. For Simpson, phylogeny was only one of several criteria for classification, but for Goodman it was the only criterion.

Goodman's commitment to cladistic classification in 1962 was deceptively modern. Like most American biologists, he was unfamiliar with the more formal cladistic approaches of Willi Hennig and his followers. He remained unaware of this group of cladists until the beginning of the 1970s. Initially, Goodman did not sharply distinguish his cladistic systematics from Simpson's evolutionary systematics, and his criticism of Simpson's approach to taxonomy was muted. Goodman's general use of the term "cladistic" is what one might expect from having read Simpson's *Principles of Taxonomy* (1961), which discussed the concept but did not present it as the theoretical foundation for an alternative approach to classification. Although he was already drawn to a purely phylogenetic classification, Goodman did not immediately abandon other aspects of Simpson's approach to systematics. He accepted Simpson's general time scale for major points of divergence in primate evolution and he continued to accept the idea of evolutionary grades. Indeed, Goodman explicitly used the idea of evolutionary grades to explain some apparent anomalies in his serological data.

Not all of the serum proteins that Goodman tested behaved alike. Unlike serum albumin, which was indistinguishable among humans, gorillas and chimpanzees, gamma globulin showed clear-cut differences. Goodman explained this anomaly with a speculative theory that fit within the general evolutionary framework provided by Simpson and Le Gros Clark, but which also had a novel immunological component. Goodman argued that mammalian evolution, in general, and primate evolution, in particular, were characterized by increased brain size, complex learned behavior, and prolonged maternal care (both before and after birth). Goodman described this pattern as an evolutionary progression of step-like grades with humans perhaps reaching a "peak of efficiency" in the process of gestation. In opossums and other marsupials (metatherians) development within the uterus was rudimentary, and most fetal development occurred in the pouch. Other mammalian groups had evolved elaborate placentas of various types that allowed longer periods of gestation. The most advanced or hemochorial placenta found in humans and apes involved an elaborate interface between maternal and fetal blood supplies. Together with prolonged gestation, Goodman argued that the hemochorial placenta was an important preadaptation for the well-developed cerebral cortex of humans and apes.

From an immunological perspective prolonged gestation and the hemochorial placenta posed significant problems, however, because they provided opportunities for the development of maternal antibodies against fetal proteins. According to Goodman, two antagonistic types of natural selection acted in mammalian evolution. Natural selection had favored more efficient exchange of gases and nutrients across the placenta. But the more intimate juxtaposition of maternal and fetal blood supplies also opened opportunities for "immunological aggression" against the fetus. Goodman reasoned that there should be strong selective pressure against variability in proteins like albumin that appear early in fetal development. This suggested a scenario where the rate of molecular evolution in albumin slowed down in the lineages with hemochorial placentas (e.g., gorillas, chimpanzees, and humans). Early in primate evolution, when gestation was shorter and the interaction between maternal and fetal blood was relatively inefficient, variation in potentially antigenic amino acid sequences of albumin would be selectively neutral. As gestation became longer and the interaction between maternal and fetal blood became more intimate, natural selection would increasingly eliminate any amino acid configurations that acted as antigens for maternal antibodies. Proteins like gamma globulin, which were produced late in fetal development or even after birth, would not be under such strict selection pressure and would, therefore, remain more variable.

Goodman's theory of molecular evolution was controversial, and he later largely abandoned it.[18] However, it played a prominent role in his thinking throughout the 1960s. It also illustrates how Goodman worked within the general framework of the evolutionary synthesis, at least during the decade of the 1960s. During this period Goodman viewed the evolution of the placenta as a progressive series of evolutionary grades. He emphasized natural selection as the primary mechanism of the molecular evolution of albumins. In the earliest versions of the theory, Goodman even tried to justify his explanation of the evolution of albumin using R. A. Fisher's models of population genetics. As more evidence accumulated supporting his claim for the close evolutionary relationships among humans and apes, Goodman had less need for his rather speculative theory of the evolution of albumin. After 1970 the theory played a diminished role in Goodman's thinking, and he eventually abandoned it.

Negotiating the Contours of Primate Evolution and Classification

Simpson played three broadly overlapping roles in Goodman's career. At various times the older biologist served as mentor, antagonist, and foil. Prior to the 1962 meeting at Burg Wartenstein, Simpson served as a kind of informal mentor, as he did for many primatologists, physical anthropologists, and molecular evolutionists. As a newcomer to the field of primate evolution and taxonomy, Goodman turned to Simpson as the leading authority in the field. He read Simpson's books beginning with the semipopular *The Meaning of Evolution* and then moving to the more technical "Principles of Classification and a Classification of the Mammals" and *The Principles of Animal Taxonomy*. He also corresponded with Simpson, both to explain his immunological technique and to seek advice. Goodman thought that he was working within the broad contours of Simpson's evolutionary systematics, and he was surprised when the older taxonomist rebuffed his revision of primate classification.

At the Burg Wartenstein conference in 1962, the different views of the two scientists became obvious and public. However, at first, Goodman tended to downplay the differences and he continued to accept some of Simpson's ideas, such as the concept of evolutionary grades. During the next decade or so, however, Goodman gradually distanced himself from many of Simpson's views. This happened in a piecemeal fashion. By the early 1970s Goodman had essentially repudiated most of his intellectual ties to the evolutionary synthesis. Looking back on their relationship in 1972, Simpson described Goodman as "an old, friendly antagonist."[19] This characterization seems to accurately capture the relationship that had developed between the two men. Goodman recalled that their encounters were never bitter or angry, but that their intellectual differences were profound. By this time Goodman was familiar with Willi Hennig's formal cladistics and he began to identify himself as a molecular cladist. This was a significant development, because although he had argued for a strictly cladistic approach to classification, before discovering Hennig and his American followers, Goodman did not articulate a strong intellectual justification for breaking with Simpson's evolutionary systematics. Once he began to identify and interact with the broader community of Hennigean cladists Goodman also began to emphasize the radical nature of his break with Simpson's primate classification.

By the mid-1970s Simpson ceased being an active participant in controversies over human evolution and primate classification. However, he continued to serve as a foil for Goodman to contrast opposing views on these topics. With cladistics and molecular systematics firmly entrenched, Goodman began to portray Simpson's evolutionary systematics as reactionary and even philosophically pre-Darwinian. For the first time he also began to attack Simpson's anthropocentrism for being "metaphysical" and the underlying intellectual source of erroneous conclusions about primate relationships. These broader philosophical questions had never been a public issue for Goodman during his face-to-face debates with Simpson. However, as Goodman began to articulate his own biocentric worldview and argue that chimpanzees should be placed with humans in genus *Homo*, Simpson's anthropocentrism and philosophical humanism became useful rhetorical targets for highlighting and justifying Goodman's own developing philosophical ideas. For example, although he emphasized the objectivity of the molecular data for supporting his proposed revision of genus *Homo*, Goodman also argued that the change should be justified on the basis of environmental ethics and conservation policy (Wildman & Goodman, 2004).

In his retrospective account, Goodman emphasized his disagreements with Simpson, while downplaying disagreements with other molecular evolutionists. But if Goodman faced opposition from Simpson, he also faced vociferous criticism from other serologists and molecular evolutionists. Alan Boyden, the leader in systematic serology, was publicly critical of Goodman's methods and was scathing in his private denunciations of the younger biologist. [20] According to Boyden, Goodman's immunodiffusion techniques were imprecise and subjective, and his theoretical explanations of protein evolution were speculative and unconvincing. Boyden ridiculed Goodman's later attempts to quantify his immnodiffusion results. In his views on taxonomy, Boyden was even more conservative than Simpson. He argued for an atheoretical approach to taxonomy that attempted to separate classification from any consideration of phylogeny or evolutionary processes. [21] Thus, on methodological, theoretical, and broader philosophical grounds, Boyden disagreed with Goodman's revision of primate classification. Even though he was at the end of his career and his views on taxonomy were not widely shared, Boyden's concerted efforts (both public and private) to undermine Goodman's reputation reveal how Goodman faced important opposition from influential members within his own specialty.

Conclusion

This episode should alert historians to the need to expand Michael Dietrich's metaphor of negotiation beyond two opposing groups of evolutionary biologists. Although for strategic reasons both Simpson and Goodman emphasized the split between molecular biologists and more traditional evolutionary biologists, there were also important issues that needed to be negotiated within each of these groups. Goodman was obviously negotiating with Boyden and other serologists over the relative merits of various immunological techniques, theories of molecular evolution, and the implications of systematic serology for taxonomic theory and practice. This was not an isolated case. Goodman also took part in spirited controversies with other molecular evolutionists on the role of natural selection in the evolution of proteins, the utility of molecular clocks for dating points of evolutionary divergence, methods of cladistic analysis, and rates of molecular evolution. Although Goodman did not emphasize these controversies in his retrospective account, they also were significant episodes in the history of primate systematics.

Considering the conflicting views of Goodman, Simpson, and Boyden illustrates the variety of meanings that "Darwinian" had in mid- and late-twentieth century systematics. All three men claimed to be part of the Darwinian lineage, but on very different grounds. According to Boyden, Darwin provided a model for modern taxonomists because he did not allow evolutionary or phylogenetic considerations to influence his classification of barnacles. Darwin's classification of the Cirripedia was sound precisely because it was an empirical study unsullied by evolutionary speculation (Boyden, 1973, pp. 211–226). This reading of history served as justification for Boyden's rejection of all three approaches to taxonomy that were contending during the 1960s and 1970s: evolutionary systematics, numerical taxonomy, and cladistics. Together with conservative taxonomists like Richard Blackwelder, Boyden argued unsuccessfully that taxonomists should construct practical classifications and that they should keep theory to a minimum. Simpson acknowledged that Darwin's taxonomy was typological and not strongly influenced by his evolutionary theory. For Simpson, Darwin's importance lay not in his taxonomic work *per se*, but in establishing an evolutionary biology that formed the intellectual foundation for the evolutionary synthesis and evolutionary systematics. It was for later evolutionary systematists like Simpson and Mayr to fully apply Darwinian principles in taxonomic research (Simpson, 1961, chap. 2, particularly p. 40). Thus, in Simpson's historical account the evolutionary synthesis and evolutionary systematics were the culmination of the Darwinian tradition. In his later writings Goodman disputed this intellectual heritage. Goodman presented Darwin as a protocladist who laid the groundwork for a purely genealogical approach to classification. From Goodman's historical perspective, Simpson was a reactionary who abandoned true Darwinian systematics and reverted to an anthropocentric and pre-Darwinian *scala naturae*. Scientists, as Polly Winsor reminds us, often use history for their own purposes (Winsor, 2004). While taking these accounts seriously, historians of biology must strive to separate the wheat from chaff. The career of Morris Goodman and his complex relationship with George Gaylord Simpson provides an insightful perspective on the shifting influence of the evolutionary synthesis during the decades following World War II.

Notes

1. Zuckerkandl (1962). The development of Zuckerkandl's evolutionary ideas has been carefully documented and analyzed by Morgan (1998).
2. The technique involved digesting proteins and using chromatography and electrophoresis to separate the resulting amino acids and peptides. The two-dimensional pattern of these products formed a "fingerprint" that could be compared among species.
3. Zuckerkandl (1962, p. 247). The same claim was made in Zuckerkandl and Pauling (1962).
4. Simpson (1964); see also Simpson (1962, p. 25).
5. Simpson (1962). Goodman told me Simpson had not reacted so critically to an earlier presentation of the immunological results at a meeting sponsored by the New York Academy of Sciences; interview with Morris Goodman conducted by the author, July 28, 2004, and available on the History of Recent Science and Technology Web site: http://hrst.mit.edu/hrs/evolution/public/goodman.html (hereafter referred to as Goodman interview [2004]). It seems likely it was the back-to-back claims of Goodman and Zuckerkandl that caught Simpson's critical attention.
6. Zuckerkandl (1987); Goodman (1996); Goodman interview (2004).
7. Zuckerkandl's comment is reported by Dietrich (1998). The relationship between the leaders of the evolutionary synthesis and molecular evolutionists is also discussed by Morgan (1998), Aronson (2002), and Hagen (1999).
8. Goodman and Moore (1971) provided an excellent illustrated description of the Ouchterlony plate method.
9. The early history of the field is described by Boyden (1953).
10. Boyden (1964). That Boyden saw his laboratory work as being part of the broader taxonomic tradition is evident in his use of the term "serological museum" to describe his collection of results; see Boyden (1958).
11. Goodman interview (2004), and Goodman (1996).
12. Simpson corresponded with several prominent serologists, including Boyden, Goodman, Allan Wilson, and Curtis Williams. The letters are in the Simpson papers at the American Philosophical Society.
13. A good example is the scathing dismissal of Simpson's approach to mammalian systematics and paleontology in Novacek (2000, p. 119).
14. Goodman interview (2004), and Goodman (1996).
15. See Mayr's comments at the end of Zuckerkandl and Pauling (1965).
16. For a detailed discussion of the correspondence between Simpson and Huxley on these issues, and on their disagreements, see Swetlitz (1995). The broader intellectual context of the two biologists' views on progress is provided by Ruse (1996).
17. For a critical comparison of the views of Huxley and Simpson, see Shanahan (2004, chapter 8).
18. For example, see the critique of Boyden (1973, pp. 187–189).
19. Simpson to Boyden, September 11, 1972, Simpson papers, American Philosophical Society.
20. For example, see Boyden (1973, pp. 187–189). Boyden wrote an even more incendiary denunciation of Goodman's research in a letter to Simpson. Interestingly, when Boyden asked Simpson to contribute a critique of Goodman's research for a serological newsletter that he edited, Simpson refused. See Boyden to Simpson, August 28, 1972, and Simpson to Boyden, September 11, 1972, Simpson Papers, American Philosophical Society.
21. Boyden (1973, chap. 7). It should be noted that Boyden was equally critical of the major schools of taxonomy: evolutionary systematics, numerical taxonomy, and cladistics. His views were shared by other conservative taxonomists such as Richard Blackwelder; see Cain (2004).

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