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Reconceiving Paleoanthropology in the Era of the Modern Evolutionary Synthesis

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ABSTRACT

The Modern Synthesis was not widely adopted by paleoanthropologists until the 1950s, but the perception has been that this event had important theoretical and methodological consequences for the study of hominid evolution. This paper presents a general historical overview of the state of evolutionary theory within paleoanthropology during the early twentieth century, the key events that led to the integration of the Modern Synthesis into paleoanthropology, and the major consequences this had. Among the most important effects were the rejection of Neo-Lamarckian and orthogenetic mechanisms to explain hominid evolution. The Modern Synthesis emphasized genetics, the centrality of natural selection as the driving force of evolution, the notion that populations are highly variable, and that evolution produced gradually evolving lineages where the boundary between ancestor and descendant species is fuzzy. The Modern Synthesis encouraged the reform of hominid taxonomy, which resulted in the dramatic reduction of hominid taxa, and influenced hominid phylogeny through such ideas as the single species hypothesis. However, historians of science and paleoanthropologists have raised questions regarding the specific influences of the Modern Synthesis and the extent to which major developments in paleoanthropological theory and practice since 1950 should be attributed to the Modern Synthesis or to a more complex range of developments.

INTRODUCTION

The Modern Evolutionary Synthesis (also called the Modern Synthesis or the Evolutionary Synthesis) marked an important development in the history of biology, but paleoanthropologists were slow to recognize its significance and to embrace it. Histories of paleoanthropology devote much attention to the discoveries of hominid[1] fossils and to debates over competing models of hominid phylogeny. While these histories refer to the fundamental contributions made by Charles Darwin and evolutionary theory as it related to the question of human evolution, there are many questions concerning the application of evolutionary theory to specific problems and episodes in the history of paleoanthropology that deserve greater examination. Peter Bowler (1986) offers an excellent examination of how evolutionary biology was employed to explain human evolution, but his book stops just at the point when the Modern Synthesis appears. Several papers in Frank Spencer's *History of American Physical Anthropology* (1982) highlight the significance of the Modern Synthesis on areas of research relating to physical anthropology and paleoanthropology during the last half of the twentieth century (see particularly the chapter by Erik Trinkaus).

More recently, Richard Delisle (1995, 2001, 2007) has investigated the influence of the Modern Synthesis on the way paleoanthropologists explained the process of hominid evolution as well as the way they approached hominid phylogeny. And Tom Gundling (2012) has written on the connections between the Modern Synthesis and theories of hominid bipedalism. In addition to historians of science,

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some paleoanthropologists have also recently drawn attention to what they see as the historical significance and scientific consequences of paleoanthropologists adopting the Modern Synthesis. Often this interest is driven by contemporary theoretical and methodological debates within paleoanthropology itself. Jeffrey Schwartz (2017) has argued that it is important for researchers to recognize that when paleoanthropologists accepted the ideas and implications of the Modern Synthesis there were certain biases introduced into the study of human evolution relating to hominid taxonomy, phylogeny, and evolutionary processes that have influenced paleoanthropology for the last half-century. Ian Tattersall (2012) also sees important consequences derived from the dominance of the Modern Synthesis within modern paleoanthropology. He has argued that the Modern Synthesis' notion of evolutionary processes and its approach to taxonomy has led many paleoanthropologists to be reluctant to identify new hominid species and genera, even when new fossil discoveries seem to demand it, and that the Modern Synthesis has influenced the methods used to distinguish hominid taxa.

Paleoanthropologists and historians have expressed some uncertainty, however, regarding the influences of the Modern Synthesis on paleoanthropological theory and practice. Robert Foley (2001) has suggested that the linear hominid phylogenies, linked to the so-called single species hypothesis, that attained prominence in the 1960s did not derive entirely from the adoption of the Modern Synthesis (as is often claimed). Instead, he argues that they originated from the progressive theories of human evolution proposed in the early twentieth century by such people as Franz Weidenreich and Wilfrid Le Gros Clark (these are discussed below), and that the new approach to hominid taxonomy and phylogeny promoted by the Modern Synthesis simply reinforced ideas already present in paleoanthropology. Richard Delisle (2001, 2007) has argued that the discovery of new hominid fossils as well as changing ideas about hominid phylogeny were as important as the adoption of the Modern Synthesis in changing paleoanthropological thinking in the 1950s and 1960s. He also argues that many of the effects that the Modern Synthesis had on paleoanthropology were the result of earlier trends already occurring in the discipline and were not due entirely to the integration of the Modern Synthesis into paleoanthropology. In this scenario, the ideas and implications of the Modern Synthesis were simply compatible with ideas and trends within paleoanthropology that predated the acceptance of the Modern Synthesis and therefore it is difficult to determine just exactly what the direct consequences were of the adoption of the Modern Synthesis by paleoanthropologists.

This paper traces the history of how the Modern Synthesis came to be integrated into paleoanthropology in the 1950s and 1960s and outlines what the main actors saw as the major consequences of this. Rather than focusing on a few aspects in great detail, it presents a broad and general overview of the subject. This will hopefully provide a useful historical context for current paleoanthropologists to understand the events of this important period, as well as establish a foundation for historians to examine more specific questions in greater detail. This paper argues that the adoption of the Modern Synthesis influenced Sherwood Washburn's formulation of the New Physical Anthropology and had important effects on the ways paleoanthropologists explained the process of human evolution. As a result, paleoanthropologists emphasized the mechanism of natural selection, adopted a population rather than a typological conception of species, and they changed the way they approached hominid taxonomy and hominid phylogeny. In order to recognize the effects of the Modern Synthesis on these questions it is essential to begin by examining the state of paleoanthropological research in the early twentieth century, which provides a context for the introduction of the Modern Synthesis, but also a contrast with the approach to paleoanthropological questions that arose after the widespread adoption of the Modern Synthesis.

PALEOANTHROPOLOGY AND EVOLUTIONARY THEORY IN THE EARLY TWENTIETH CENTURY

While evolutionary biology is a central component of paleoanthropology today, that was not always the case. During the first half of the twentieth century, the relationship between paleoanthropology and evolutionary biology was complex. It is important to recognize that throughout the early twentieth century most of the people who excavated hominid fossils were trained as paleontologists and many of the scientists who analyzed and described these fossils were trained as anatomists, physical anthropologists, or vertebrate paleontologists. They devoted most of their attention to producing detailed anatomical descriptions of newly discovered fossils and to determining their geological (stratigraphic) context and identifying the animal fossils and archaeological artifacts that were associated with a hominid fossil. In many instances these anatomists and anthropologists did not employ evolutionary mechanisms or theories to interpret hominid fossils. They simply relied on skeletal morphology and the geological age of hominid fossils to arrange them in plausible evolutionary phylogenies (see, for example, Hammond, 1988; Theunissen, 1989; Trinkaus and Shipman, 1993).

There were, of course, biologists and anthropologists following the publication of Charles Darwin's *On the Origin of Species* in 1859 who discussed schemes of human evolution and used evolutionary theory to interrogate the meaning of the growing hominid fossil record. However, as Peter Bowler (1983) has emphasized, it is important to note that while the vast majority of biologists supported the idea of biological evolution by the turn of the twentieth century, there were several competing theories of how evolution operated. Some biologists adopted Darwin's mechanism of natural selection as the primary cause for species change, but a great many biologists and anthropologists promoted alternative theories. One of the most widely supported evolutionary theories during the early twentieth century was Neo-Lamarckism.

Neo-Lamarckism utilized the idea of use-inheritance that was first proposed by the French naturalist Jean Baptiste de Lamarck at the beginning of the nineteenth century. Central to Neo-Lamarckism was the notion that the anatomy and physiology of an organism could be directly affected by environmental conditions and that these changes could be passed on to the next generation. Some proponents of Neo-Lamarckism, influenced by studies of the development of embryos, suggested that evolution occurred as the result of the addition of new stages of growth in an individual before it reached maturity. An appealing aspect of Neo-Lamarckism emphasized by many of its proponents was the idea that life was purposeful and creative, that life could direct its own evolution. This contrasted sharply with the undirected, even random, nature of Darwinian evolution by natural selection (see Bowler, 1988: Chapter 4).

Orthogenesis offered yet another conception of how evolution operated. Supporters of orthogenesis argued that evolution progressed along a particular, often linear, course that was directed by forces internal to an organism. Orthogenesis viewed the evolutionary process as progressing toward a predetermined fixed goal. Unlike Darwinian and Neo-Lamarckian conception of evolution, the orthogenetic process of evolution was not adaptive, since it functioned independent from what was happening in an organism's environment. As a result, these orthogenetic processes could drive a species to extinction. Some paleontologists were drawn to orthogenesis because it seemed to explain certain evolutionary trends that they perceived in the fossil record of some groups of organisms.

In order to understand the consequences of the adoption of the Modern Evolutionary Synthesis by paleoanthropologists after 1950, it is essential to examine the study of human evolution during the first half of the century. Many of the paleoanthropologists during this period who discussed the evolutionary mechanisms involved in human evolution relied on Neo-Lamarckian or orthogenetic processes. The English anatomist and anthropologist Frederic Wood Jones, in his book *Man's Place among the Mammals* (1929), employed Neo-Lamarckian mechanisms to explain the course of hominid evolution. Those paleoanthropologists who relied on Neo-Lamarckian conceptions of hominid evolution often argued that primate evolution was driven by their response to living in a challenging arboreal environment, or in the case of early hominids it was living on the savannah. One consequence of this way of understanding the factors driving hominid evolution was the widespread idea among paleoanthropologists that similar environments and challenges resulted in the parallel evolution of similar anatomical traits in the long separated evolutionary lineages of apes and hominids. The Neo-Lamarckian view of evolution adopted by these paleoanthropologists led them to argue than an organism's behavior affected its evolution, thus similar behaviors would lead to the evolution of similar anatomical structures in entirely separate lineages, since these structures would serve similar functions in each lineage (Bowler, 1986: 190–193).

One influential consequence of this way of explaining human evolution was the popularity of the pre-sapiens hypothesis among some leading paleoanthropologists during the early twentieth century. The pre-sapiens hypothesis argued that the ape and human lineages had separated a very long time ago, as early as the Miocene or even the Oligocene. Significantly, this meant that humans had not evolved from an ape ancestor but instead from an earlier more generalized form of primate and thus humans had not passed through an ape stage in the course of our evolution. The ape and hominid lineages evolved separately, but this required a significant degree of parallel evolution in these two lineages, in order to explain the many anatomical similarities between apes and humans that would otherwise be explained by humans having evolved from a recent ape ancestor. Paleoanthropologists Marcellin Boule and Henri-Victor Vallois were influential advocates of the pre-sapiens hypothesis in France, as was the anatomist Arthur Keith in England and the Kenyan paleoanthropologist Louis Leakey. Meanwhile, other paleoanthropologists embraced ideas from orthogenesis in their explanations of human evolution. A leading example is the American paleontologist Henry Fairfield Osborn. Osborn outlined an orthogenetic view of human evolution in *Men of the Old Stone Age* (1915) and later formulated a version of orthogenesis he called aristogenesis (Osborn 1934). Ernest Hooton, the influential professor of physical anthropology at Harvard University, invoked Neo-Lamarckian and orthogenetic mechanisms in his book *Up from the Apes* (1931) in order to explain what he saw as progressive and non-adaptive trends in primate evolution.

Wilfrid Le Gros Clark, professor of anatomy at Oxford University, is a particularly instructive example of how Neo-Lamarckian and orthogenetic ideas were applied to the problem of human evolution during this period. In his book, *Early Forerunners of Man* (1934), Le Gros Clark deployed Neo-Lamarckian and especially orthogenetic mechanisms to explain the course of hominid evolution. Like other paleoanthropologists at this time, he believed that parallel evolution was a common feature in the evolution of life on earth.

> "The fact is that the minute and detailed researches which have been carried out by comparative anatomists in recent years have made it certain that parallelism in evolutionary development has been proceeding on a large scale and is no longer to be regarded as an incidental curiosity which has occurred sporadically in the course of evolution" (Le Gros Clark, 1934: 6).

Moreover, Le Gros Clark believed that non-adaptive characters could be produced independently in separate evolutionary lineages. He argued that phylogenetically related groups inherited a biological tendency to evolve along similar trajectories.

> "This conclusion inevitably leads to the conception of an orthogenetic trend of evolution dependent upon an inherent tendency in the common progenitor to the production of similar features in divergent groups of descendants" (Le Gros Clark, 1934: 79).

Le Gros Clark then specifically applied these orthogenetic trends to explain what he perceived as examples of parallel evolution within the primates. In his view,

> "It seems certain that the instances of parallelism in the evolution of the Primates…are to be interpreted satisfactorily only by the conception of definite predetermined trends of development—that is, by the conception of Orthogenesis. This conception puts the onus of evolutionary progress more on the germ-plasm and regards the influence of the environment as of somewhat secondary importance" (Le Gros Clark, 1934: 288).

Among the evolutionary tendencies that he identified in the primates that were not the product of adaptive pressures was the evolution of the brain as well as their distinctive dentition. Le Gros Clark argued that there was a general trend toward the evolution of a larger brain in all primates and that this trend was inherited from the earliest primate ancestor.

> "The line of evolution of the Anthropoidae has been marked by the successive branching off of specialized groups from a central stem in which a progressive expansion of the brain has been accompanied by the retention of a bodily structure of a remarkably generalized type. It is this main stem which culminated in the appearance of Man himself" (Le Gros Clark, 1934: 286).

While there were anthropologists during the first half of the twentieth century who supported Darwin's version of evolution driven by natural selection, these examples show that some of the most influential paleoanthropologists at this time emphasized Neo-Lamarckian and orthogenetic mechanisms when they discussed hominid evolution. It is within this context that we need to examine the process by which the Modern Evolutionary Synthesis displaced these earlier approaches to explaining human evolution. It is not possible here to present a detailed history of the origins of the Modern Synthesis; there are excellent works on this subject that recount these events (Mayr and Provine, 1980; Smocovitis, 1996). The Modern Synthesis emerged during the second quarter of the twentieth century as a result of developments in Mendelian genetics, research into chromosomes, and the application of population genetics to evolutionary biology. Some field biologists were beginning to view species as composed of local populations, with their own distinctive characteristics, that were reproductively isolated from other populations. These biologists believed geographical isolation was essential for the emergence of new species by a process of splitting.

At the same time, J.B.S. Haldane (1924, 1932) and Ronald Fisher (1930) in Britain and Sewall Wright (1931) in the United States were using mathematics to show how gene frequencies could change in a population due to natural selection. Their work demonstrated that natural selection worked through the mechanism of Mendelian inheritance. Wright suggested that small random genetic changes in small local populations, what he called genetic drift, could greatly increase the field of variability available for natural selection to operate upon. As a consequence, natural selection would occur most readily in small isolated populations. Theodosius Dobzhansky, a Ukrainian born geneticist at Columbia University, also sought to integrate Mendelian genetics and population genetics into Darwin's theory of evolution by natural selection in his book *Genetics and the Origin of Species* (1937). Dobzhansky also sought to bring the taxonomic and morphological concept of the biological species into line with these new ideas. Soon thereafter, German biologist Ernst Mayr, who had joined the staff of the American Museum of Natural History in 1931, published *Systematics and the Origin of Species* (1942). Mayr brought his experience as a field biologist to the task of showing how Mendelian genetics and natural selection operating on populations inhabiting specific environments could explain the evolution of new species. While these mechanisms could explain microevolution, the small gradual changes occurring within a species over relatively short time periods, a question still remained of whether these processes could explain the macroevolutionary patterns observed in the fossil record. American paleontologist George Gaylord Simpson tackled this question in *Tempo and Mode in Evolution* (1944). Simpson showed that the microevolutionary processes described by Dobzhansky and Mayr could explain the macroevolutionary trends visible in the fossil record, and in doing so introduced the ideas of the Modern Synthesis and population genetics to paleontologists (for a more detailed account see Mayr and Provine, 1980; Smocovitis, 1996).

These works asserted that natural selection was the mechanism driving evolution and they convincingly rejected Neo-Lamarckism and orthogenesis as valid theoretical alternatives. This growing consensus, called the Modern Evolutionary Synthesis, broadly argued that nearly all evolutionary change was the result of the accumulation of small genetic changes in a population, which were acted upon by natural selection. This resulted in lineages that gradually evolved over long periods of time as species became increasingly well adapted to their environments. The proponents of the Modern Synthesis thought that speciation mostly occurred when a population within a species became geographically isolated and thus could split off and evolve in a new direction. While many biologists and geneticists quickly accepted the Modern Synthesis, anthropologists and paleoanthropologists were slow to adopt it. When they did, there were a number of important consequences.

INTEGRATING THE MODERN EVOLUTIONARY SYNTHESIS INTO PALEOANTHROPOLOGY

Two episodes offer some insights into the relationship that existed between the Modern Synthesis and the discipline of paleoanthropology prior to 1950. When the Society for the Study of Evolution was founded in 1946, as a new international body promoting the Modern Synthesis, no paleoanthropologists participated in its creation. This was despite the fact that some of the founders of the Modern

Synthesis were calling for anthropology to incorporate the Synthesis' view of evolution into the discipline. The lack of interest among anthropologists may be explained by their reluctance to reduce anthropology to biology (see Smocovitis, 2012: 109–110). The second episode was an international meeting held in Paris in April 1947 organized by the Centre National de la Recherche Scientifique (C.N.R.S.) and the Rockefeller Foundation, which brought together paleontologists, paleoanthropologists, and geneticists. Among those attending the meeting were J.B.S Haldane, George Gaylord Simpson, and the French population geneticist Georges Teissier, all of whom promoted the Modern Synthesis view of evolution. However, there was a contingent of paleoanthropologists at this meeting, including Camille Arambourg, Henri-Victor Vallois, Jean Piveteau, and Pierre Teilhard de Chardin, who resisted the Modern Synthesis and persisted in advocating Neo-Lamarckian or orthogenetic versions of evolution (Arambourg, 1950).

Yet, already there were steps being taken to bring the ideas of the Modern Synthesis into paleoanthropology. In 1944, Dobzhansky published a paper applying the Modern Synthesis to hominid taxonomy as well as to the concept of species and race as these applied to humans. Dobzhansky applied the population genetic view of species to argue that humans should be understood as a single polytypic species, with races representing populations displaying geographical variations in morphology. Likewise, he saw the *Pithecanthropus* specimens from Indonesia and the *Sinanthropus* specimens from China as racial variations of a single hominid species *Homo erectus* (1944: 257). Another important source was George Gaylord Simpson's *Meaning of Evolution* (1949), written as a general introduction to the Modern Synthesis, which was widely used in introductory physical anthropology courses and influenced many anthropologists of the post-World War II generation. But one of the first anthropologists to realize the importance of integrating the Modern Synthesis into paleoanthropology was Sherwood Washburn. Washburn studied physical anthropology under Ernest Hooton at Harvard and while he was a professor at Columbia University in the 1940s he got to know Dobzhansky and George Gaylord Simpson. Dobzhansky was an important influence on Washburn's views about evolution at this time. Washburn left Columbia to become professor of anthropology at the University of Chicago in 1947 and by this time he was actively involved in utilizing the ideas of the Modern Synthesis to tackle a wide variety of problems relating to human evolution.

One influential step in the process of integrating the Modern Synthesis into paleoanthropology began in 1946 when Washburn initiated the Summer Seminars in Physical Anthropology. The Summer Seminars were designed to bring together researchers and students to discuss new ideas and research methods in physical anthropology. The seminars met in New York City every summer from 1946 to 1951, then in Boston in 1953 and in Washington, D.C., in 1955. The seminars were financially supported by the Viking Fund (renamed the Wenner-Gren Foundation for Anthropological Research in 1951), which was directed by Paul Fejos. Washburn and Fejos had become friends when Washburn was at Columbia and under Fejos' leadership the Wenner-Gren Foundation became an important supporter of paleoanthropological research (Szathmáry 1991). From the start the Summer Seminars promoted a new vision of physical anthropology, one that turned away from description and typology and instead emphasized specific well-defined problems and collaborative research with biologists from different specializations, especially genetics, evolutionary biology, and primate studies. One of the major themes of the seminars was human evolution (Mikels-Carrasco, 2012).

The Summer Seminar meeting of 1951 was devoted primarily to defining modern physical anthropology as a science that involved evolutionary biology, hominid paleontology, primate studies, anthropometry, genetics and human variation (race), human ecology, and applied physical anthropology (forensics). The Modern Synthesis view of evolution was presented as the unifying theoretical framework for this new physical anthropology. As a supplement to the Summer Seminars, Washburn also initiated the *Yearbook of Physical Anthropology*. It was created to report the events of the Summer Seminars, to reprint important papers published in foreign journals, and to summarize the state of the field. The first volume appeared in 1946 with Gabriel Lasker as its editor and the *Yearbook* served as an important means of promulgating this new conception of physical anthropology. In addition to the Summer Seminars, the International Symposium on Anthropology, which was held in New York City in June 1952, is important because it was also designed to make the case for why the Modern Synthesis approach to evolution should be integrated into anthropology. The symposium was sponsored by the Wenner-Gren Foundation and Fejos and Washburn were influential in its planning (the symposium is why there was no Summer Seminar in 1952). The conference resulted in the *Anthropology Today* volume, edited by Alfred Kroeber (1953), which placed great emphasis on the Modern Synthesis and Washburn's New Physical Anthropology (see especially Washburn, 1953).

The roots of the New Physical Anthropology can be traced back to Washburn's research as a graduate student in physical anthropology at Harvard University, when he began thinking about the connections between primatology, paleoanthropology, and physical anthropology. Influenced by the Modern Synthesis, he saw the need to replace the old typological and descriptive physical anthropology of the early twentieth century, which relied upon anthropometry to identify and characterize static human races. He imagined instead a new kind of physical anthropology that would rely upon the study of genetics, morphology, and function in order to produce a dynamic view of humans. In addition, Washburn became interested in a developmental and experimental approach to investigating functional anatomy. Washburn's New Physical Anthropology emphasized the study of form, function, and behavior. It relied on an interdisciplinary approach to investigating human evolution that employed ideas drawn from the

Modern Synthesis, primate studies, physical anthropology, and functional anatomy, as well as archaeology and cultural anthropology. The New Physical Anthropology focused on the processes by which anatomical, morphological, and evolutionary changes happen. It also approached human races as populations and not as natural morphological types, a perspective that was consistent with the Modern Synthesis view of biological species (Washburn, 1951; 1953).

Washburn emphasized the study of adaptive complexes (head, thorax and arms, pelvis and legs) and the selective pressures that acted on these complexes in the course of hominid evolution. He argued that hominid evolution was driven in large part by the shift to bipedal locomotion and later by the development of culture and the use of tools that resulted from the emergence of a larger brain. Washburn's interest in functional anatomy and human evolution led him to apply discoveries made about primate behavior in the wild to his ideas about human evolution, which resulted in the influential Man the Hunter hypothesis. Washburn's integration of the Modern Synthesis into physical anthropology, which was a central element of the New Physical Anthropology, created the possibility for new approaches and new theories of human evolution, and it expanded the range of research topics in physical anthropology (Mikels-Carrasco, 2012).

While Washburn's New Physical Anthropology and the Summer Seminars served as one means by which the Modern Evolutionary Synthesis was introduced into the discipline of paleoanthropology, historians and anthropologists have focused a great deal of attention on the 1950 meeting of the Cold Spring Harbor Symposium on Quantitative Biology. The Symposium, titled "The Origin and Evolution of Man," was organized by Milislav Demerec, the director of the Cold Spring Harbor Laboratory, with the assistance of Dobzhansky and Washburn. Many prominent anthropologists, geneticists, and evolutionary biologists took part and the topics covered at the meeting included human origins, hominid taxonomy, the application of population genetics to anthropology, and the genetic analysis of human racial traits. Among those attending were William Howells, Ernst Mayr, George Gaylord Simpson, Richard Lewontin, Alfred Kroeber, Earnest Hooton, Wilton Krogman, Carleton Coon, Joseph Birdsell, Ashley Montagu, T. Dale Stewart, and Theodore McCown. The speakers presented a wide-ranging critique of the disciplines of physical anthropology and paleoanthropology. These critiques included the way that hominid taxonomy and phylogeny had been handled in the previous half century. The typological conception of human races also came under fire. A major message of the symposium was that the Modern Synthesis' emphasis on populations, genetics, and evolutionary processes needed to be incorporated into physical anthropology and paleoanthropology. The implications of doing so were wide ranging.

HOMINID EVOLUTION, TAXONOMY, AND PHYLOGENY UNDER THE MODERN SYNTHESIS

Ernst Mayr's paper at the Cold Spring Harbor Symposium has been considered one of the most influential of those presented. He vigorously criticized paleoanthropologists for devoting too little attention to evolutionary mechanisms and processes when interpreting the hominid fossil record and explaining human evolution. He was equally critical of the way paleoanthropologists had constructed hominid phylogenies and their taxonomic practices. He observed that "there is less agreement on the meaning of the categories species and genus in regard to man and the primates than perhaps in any other group of animals." He went on to suggest that

> "an effort should be made to give the categories species and genus a new meaning in the field of anthropology, namely, the same one which in recent years has become the standard in other branches of zoology" (Mayr, 1951: 109).

Mayr's conception of evolution, drawn from the Modern Synthesis, relied upon the geographical isolation of populations within a species that then went on to evolve into new species. His notion of species left them as taxonomically fuzzy entities, where in gradually evolving lineages it was essentially arbitrary how one distinguished one species from another in the fossil record. As a result, Mayr argued for the need to reform hominid taxonomy. Moreover, he supported the single species hypothesis first suggested by Theodosius Dobzhansky.

Dobzhansky (1944) had argued that in the course of human evolution only one species of hominid had existed at any one time. In his view, hominids consisted of a single evolving lineage that possessed considerable geographical variation. This conception of human evolution was influenced by German anthropologist Franz Weidenreich's polycentric theory of human evolution. Weidenreich argued that several racially distinct geographical populations of hominids throughout the Old World had evolved from *Homo erectus* to *Homo sapiens*, yet at any one time these populations remained part of a single species due to the small amounts of genetic exchange between these geographically separated populations. Dobzhansky considered these regional hominid populations to be sub-species, not species, since they were not reproductively isolated (see also Dobzhansky, 1955, 1962).

Like Dobzhansky, Mayr suggested that only one species of hominid had existed at any one time in the course of hominid evolution. He recognized that geographical (racial) variation existed among humans, but he considered these variations to be taxonomically trivial. As a result, Mayr portrayed hominid evolution as a single constantly changing lineage, with no side branches, that consisted of highly variable members of a single species. This implied that the boundaries between species were fuzzy and that species were ephemeral. Mayr also followed Dobzhansky in promoting the idea that there was considerable intraspecies variability. Given all of this, Mayr proposed a radical revision of existing hominid taxonomy to bring it into line with the Modern Synthesis. He argued that the large number of hominid genera and species be reduced to just three successive species—*Homo transvaalensis* (comprising the australopithecines), *Homo erectus*, and *Homo sapiens* (Mayr, 1951).

George Gaylord Simpson also complained about hominid taxonomy. As early as 1949, Simpson had characterized primate and hominid taxonomy as a "mess" and he attributed this to the fact that the anatomists and anthropologists who had named species were unfamiliar with zoological classification (1949: 81). He returned to this issue in a paper presented at the Wenner-Grenn Foundation symposium on "Classification and Human Evolution" that was organized by Sherwood Washburn in 1962. He again criticized the way paleoanthropologists had named hominid taxa. He observed that the definition of a taxon had often been "only a description of an individual 'type' with no regard for or even apparent consciousness of the fact that taxa are populations." He stated that the morphological differences between some hominid specimens had often been "enormously exaggerated" by paleoanthropologists and he concluded by saying that "Many fossil hominids have been described and named by workers with no other experience in taxonomy" (1963: 6).

Just to give some sense of the state of hominid taxonomy at the time, American primate paleontologist Elwyn Simons (1972) noted that prior to the application of the principles of the Modern Synthesis to hominid taxonomy there were nine genera that were later subsumed into *Australopithecus* and seventeen genera that were subsumed into *Homo*. Simpson (1945) had already argued not only that the Asian fossils classified under *Pithecanthropus* and *Sinanthropus* should be collapsed into a single genus, but also that these specimens should be classified in the genus *Homo*. In all of his publications from 1949 onward, Simpson argued that the same evolutionary processes that were employed to explain animal evolution also applied to primate and hominid evolution (Laporte, 1991). Simpson delivered the keynote lecture at the Cold Spring Harbor Symposium in 1950. In addition to applying the Modern Synthesis to the problem of hominid evolution and rejecting orthogenetic and Neo-Lamarckian mechanisms, he argued that paleoanthropologists should not rely on the comparative morphology of living primates when attempting to reconstruct their evolutionary history. Instead, they had to take time, geography, and environmental conditions into consideration. Simpson also argued that paleoanthropologists needed to recognize the distinction between parallel and convergent evolution (Simpson 1951).

Not all paleoanthropologists embraced these taxonomic and phylogenetic implications of the Modern Synthesis of course. In France, Henri-Victor Vallois continued to support the pre-sapiens hypothesis with its multiple hominid lineages and Louis Leakey only abandoned the pre-sapiens hypothesis in the 1960s. German paleoanthropologist Gerhard Heberer also continued to promote the idea of the parallel evolution of several distinct hominid lineages. These included several diverging australopithecine lineages as well as *Homo* lineages, which included an archanthropine (*Pithecanthropus*/*Sinanthropus*) line, a paleoanthropine line; and a sapiens line (Heberer 1959). But other paleoanthropologists accepted the principles of the Modern Synthesis and began applying them to problems relating to hominid evolution. Wilfrid Le Gros Clark, who had promoted an orthogenetic conception of hominid evolution since the 1930s, converted to the Modern Synthesis' understanding of evolution in *Fossil Evidence for Human Evolution* (1955), although he agreed with Simpson that a limited amount of parallel evolution had occurred, but he believed such cases had to be adaptive. Le Gros Clark (1958) adopted the taxonomic implications of the Modern Synthesis, rejecting the existing plethora of different hominid genera and species and describing *Australopithecus* and *Homo* as genera with considerable variation.

German anthropologist Emil Breitinger (1957) also accepted the Modern Synthesis's conception of biological species and taxonomy and he argued for abandoning typological thinking in physical anthropology. This led him to argue that the Neanderthals should be seen as a polytypic species that displayed regional variation. The Modern Synthesis as well as the New Physical Anthropology of Sherwood Washburn soon began to influence American paleoanthropologists. Harvard University anthropologist William Howells promoted the Modern Synthesis's view of hominid evolution in his widely read book *Mankind in the Making* (1959) as did University of Pennsylvania anthropologist Carleton Coon in his controversial *The Origin of Races* (1962). Coon's book contained a mixture of the old typological approach to identifying and characterizing human races with the principles of the Modern Synthesis. Coon attempted to explain the development of human racial variation through population genetics and natural selection producing adaptation to local environmental conditions. But Coon still retained the system of racial classification and typological thinking about race that was rejected by Washburn, Dobzhansky, and the other proponents of the Modern Synthesis.

One of the most vocal advocates of the new perspective on hominid evolution offered by the Modern Synthesis was Charles Loring Brace. Brace studied physical anthropology under William Howells at Harvard in the 1950s. By the early 1960s he was applying the principles of the Modern Synthesis and of the New Physical Anthropology to the notion of human races and to hominid evolution. He expounded his vision of hominid evolution in *Stages of Human Evolution*, first published in 1967 with the fifth edition appearing in 1995. Brace was an influential advocate of the single species hypothesis. In the first edition of the book, he asserted that all of the known hominid species composed a single evolving lineage with no side branches. Brace argued that humans had evolved through four morphological stages: australopithecine, pithecanthropine, Neanderthal, and modern human. He believed the transitions between stages occurred essentially simultaneously across different geographic areas as a result of cultural diffusion and gene flow between populations. This view of human evolution relied on the competitive exclusion principle, the idea that culture was the best way to exploit any ecological niche, and since culture allowed humans to exploit all ecological niches there would be no cause for speciation events. Once hominids adopted culture, selective pressure led them to evolve in similar ways and rates everywhere, since any important cultural and technological developments would be shared by all other groups, thus maintaining the unity of the species at each stage of evolution (Brace, 1967).

Brace initially believed that the australopithecines must have possessed tools and a rudimentary culture in order to survive, but he later had to change his thinking. Richard Leakey's discovery of KNM-ER 3733 and KNM-ER 406 at Lake Turkana, two clearly different hominid species that coexisted in geologic time, posed a serious problem for the single species hypothesis and this forced Brace in later editions of the book to accept one speciation event early in hominid evolution and to argue that the competitive exclusion principle was less effective during this phase of hominid evolution because culture was less prevalent and had less adaptive effect. And after the discovery of *Australopithecus afarensis*, Brace defended the single species hypothesis by arguing that since the australopithecines were the first terrestrial hominids and because the australopithecines lacked culture (tool-use) and probably lived by scavenging, a number of local species could have evolved. However, he continued to argue that during the course of the Pleistocene, from the emergence of *Homo erectus* to the appearance of *Homo sapiens*, hominid evolution consisted of a single evolving lineage with only one species living at any one time, with no extinctions or side branches.

Even before Brace had been forced to accept more than one australopithecine lineage, the South African paleoanthropologist John Talbot Robinson introduced an important revision to what some saw as Mayr's oversimplified version of hominid taxonomy. Robinson examined the South African australopithecine fossil record from the perspective of the Modern Synthesis, but he was forced to recognize the robust and gracile types as taxonomically distinct (Robinson, 1953, 1954). He suggested that the competitive exclusion principle did not apply to australopithecines because they had not yet developed culture (stone tool technology). "The Australopithecines in the initial phases of their evolution will have had no more than a rudimentary level of culture, hence the slowing down of the rate of speciation will not have applied" (Robinson, 1963: 394–395). But he agreed with the reduction of hominid taxa brought about by the Modern Synthesis.

Another prominent South African paleoanthropologist, Phillip Tobias, also rejected the single species hypothesis, at least for the earliest stages of hominid evolution. He suggested that from an unknown ancestor at least one speciation event had occurred and two main hominid lineages had diverged, one leading from *Australopithecus boisei* to *Australopithecus robustus* and the other leading from *Australopithecus africanus* to *Homo habilis* and then to more recent members of the genus *Homo*. Like Robinson, Tobias suggested this might partly be due to the fact that the australopithecines had no culture in the form of stone tools (Tobias, 1965, 1967). Even Ernst Mayr (1963) had to eventually admit more than one hominid lineage was present within the australopithecines. But Milford Wolpoff continued to support the single species hypothesis for the entire hominid fossil record into the 1970s. He argued that the gracile and robust australopithecines belonged to one species and he rejected the argument that their differences were based on adaptation due to differences in diet or culture. Like Brace, he supported a hominid phylogeny consisting of only one lineage leading from *Homo erectus* to the Neanderthals and on to modern humans (Wolpoff, 1968, 1971).

Another significant consequence of the Modern Synthesis was that paleoanthropologists increasingly began to examine and explain specific morphological features in hominids as the product of adaptations brought about through natural selection. A prominent early example of this was F. Clark Howell's innovative reassessment of the Neanderthals conducted in the 1950s. Howell studied under Sherwood Washburn at the University of Chicago where he absorbed the principles of the Modern Synthesis and Washburn's New Physical Anthropology. In a series of papers Howell applied these principles to arrive at a new interpretation of the Neanderthal fossil record. He began from the perspective of the Neanderthals as a highly variable population that had adapted to their local environmental conditions. He identified an older Generalized Neanderthal group, living during the Riss-Würm interglacial period, that possessed anatomical traits similar to those of modern humans. He then identified a later cold weather adapted "classic Neanderthal" group living in Western Europe in which some features of the earlier Neanderthals were modified and exaggerated. He associated these exaggerated traits with genetic isolation during the Würm glacial period and explained them as adaptations to the extremely cold conditions (Howell, 1951, 1952, 1957).

CONSEQUENCES AND CONCLUSIONS

Through the 1950s and 1960s paleoanthropologists generally adopted the principles of the Modern Evolutionary Synthesis and the related ideas of Sherwood Washburn's New Physical Anthropology. Paleoanthropology was changing in many other ways at this time. The hominid fossil record was rapidly expanding, radiometric dating methods provided more reliable dates for fossils, and molecular anthropology was just beginning to offer a new method for investigating primate evolution. The extent to which the many changes that were occurring in the study of hominid evolution were due to the adoption of the Modern Synthesis by paleoanthropologists is therefore a historically complex question. Yet, the fact that Theodosius Dobzhansky, Ernst Mayr, and George Gaylord Simpson, who were key figures in formulating the Modern Synthesis, also played a significant role in applying it to central questions of human evolution indicates that the Modern Synthesis had to be taken seriously by paleoanthropologists after the Cold Spring Harbor Symposium of 1950. Sherwood Washburn's explicit reliance upon the Modern Synthesis in his New Physical Anthropology also demonstrates the growing importance and influence of the Modern Synthesis within paleoanthropology and physical anthropology.

The significance of the Modern Synthesis within paleoanthropology can also be traced in the criticisms some scientists have made of its effects on the discipline. Ian Tattersall (2012) has argued that one lasting effect of the dominance of the Modern Synthesis within paleoanthropology has been a reluctance among researchers to identify new species and genera of hominids, even when new fossil discoveries seemed to require it. Indeed, Tattersall has suggested that some paleoanthropologists have even resisted assigning newly discovered fossils a taxonomic designation out of a fear of perpetuating the bad former practices of creating a new species or even genus for each new hominid fossil. One often cited example of this is the debate that arose over the creation of a new taxon for *Homo habilis* in 1964. Many paleoanthropologists, working within the Modern Synthesis' view of species, taxonomy, and phylogeny, argued that there was "insufficient morphological space" between the gracile australopithecines and *Homo erectus* for this new species. Jeffrey Schwartz (2017) also believes the Modern Synthesis has had unfortunate effects on the way paleoanthropologists have approached hominid taxonomy and phylogeny.

The historical evidence suggests there were several significant consequences that can be traced at least in part to the integration of the Modern Synthesis into the study of hominid evolution. Paleoanthropologists finally rejected the Neo-Lamarckian and orthogenetic conceptions of hominid evolution that had been so prevalent during the first half of the twentieth century. This not only led to the abandoning of Neo-Lamarckian and orthogenetic mechanisms that had been invoked to explain the processes driving evolution, but also influenced ideas about hominid phylogeny such as the widespread belief in parallel evolution. The Modern Synthesis placed great emphasis on genetics, the centrality of natural selection as the driving force of evolution, the notion that species are composed of populations that are highly variable (polytypic), and that evolution produces gradually evolving lineages where the boundary between ancestor and descendant species is fuzzy. The Modern Synthesis encouraged the push to bring hominid taxonomy into conformity with its central tenets, which resulted in the dramatic reduction of hominid taxa. These factors combined with ideas such as the competitive exclusion principle led to the promotion of the single species hypothesis by several paleoanthropologists, but even those who were unwilling to accept such a simple view of human evolution were still induced to bring their ideas about hominid phylogeny into line with the Modern Synthesis' understanding of evolution. The simplification of hominid taxonomy and innovations within hominid phylogeny, such as the single species hypothesis, even if influenced by other developments in paleoanthropology, were often defended on the basis of the new way of thinking about species and the evolutionary process derived from the Modern Synthesis.

The Modern Evolutionary Synthesis also had an important influence on physical anthropology by redefining the concept of race. Nineteenth and early twentieth century anthropology promulgated a conception of human races that was typological. Races were distinguished by observable morphological traits and represented natural types that were relatively fixed (see Stepan, 1982; Manias, 2013). Earnest Hooton, the influential professor of anthropology at Harvard University, exemplifies this tradition. He defined race as

> "a great division of mankind, the members of which, though individually varying, are characterized as a group by a certain combination of morphological and metrical features, principally non-adaptive, which have been derived from their common descent" (Hooton, 1926: 76).

The British born American physical anthropologist Ashley Montagu reflected the change in thinking about human races brought about by the Modern Synthesis in his paper presented at the Cold Spring Harbor Symposium in 1950. He defined race as "one of the group of natural populations comprising the species" (1951: 317) and he emphasized that the concept of race was a statistical one that applied to populations and, depending on what traits were selected by the investigator, the resulting races would vary.

It is important to note that new ideas about how evolution operated affected paleoanthropology beginning in the 1970s. The theory of punctuated equilibria, proposed by Stephen J. Gould and Niles Eldredge in 1972, challenged some central tenants of the Modern Synthesis. Rather than the gradually evolving lineages, with the fuzzy essentially arbitrary boundaries separating an ancestral species from its descendant, Gould and Eldredge argued that evolution occurred by periods of rapid (punctuated) evolution separated by long periods of stasis. They argued that species are real, not just conventions. Gould rejected the "ladder of progress" conception of human evolution and he promoted instead a view of hominid phylogeny that was more akin to a bush than a tree (Gould and Eldredge, 1972; Gould, 1976; Pievani, 2012). Gould and Eldredge criticized C. Loring Brace's linear hominid phylogeny based upon the single species hypothesis, and soon paleoanthropologists also began to adopt the punctuated equilibria view of evolution and applied it to hominid evolution. The discovery of many new hominid fossils during the 1950s and 1960s led Ian Tattersall and Niles Eldredge to assert that the Modern Synthesis' view of evolution did not match the evidence from the hominid fossil record. They argued instead that the punctuated equilibria view of evolution was a better fit (Eldredge and Tattersall, 1975; Delson et al., 1977). By this time Willi Hennig's phylogenetic systematics (cladistics) was also beginning to influence paleoanthropologists, especially after the appearance an English translation (Hennig, 1950, 1966). Tattersall and Eldredge introduced cladistics and punctuated equilibria into hominid systematics and this new approach began to be adopted by other paleoanthropologists, such as Bernard Wood (1984), although Loring Brace, Phillip Tobias, and others criticized this new approach. Tattersall's application of cladistics and punctuated equilibria to interpreting the hominid fossil record led him to recognize a large number of diverse hominid species and many adaptive radiations, more than was recognized by proponents of the Modern Synthesis view of hominid evolution and taxonomy.

There are still many aspects of the influences of the Modern Synthesis upon paleoanthropological theory and practice that have not been examined by historians or paleoanthropologists. Detailed studies of how the Modern Synthesis was integrated into paleoanthropology, the debates that emerged among paleoanthropologists over the value of this new conception of evolutionary processes, and the different ways that paleoanthropologists employed ideas from the Modern Synthesis in addressing specific problems relating to hominid evolution, would illuminate many issues existing within paleoanthropology today.

ENDNOTES

[1]In contemporary paleoanthropology 'hominin' has replaced the formerly used 'hominid' but I will retain the term hominid throughout in order to remain consistent with the use of the term in the primary sources discussed here.

STATEMENT ON USE OF AI

I assert that no AI related help was used in preparing my paper.

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