

Evolutionary theory, systematics, and the study of human origins

Ian Tattersall

Division of Anthropology, American Museum of Natural History, 200 Central Park West, New York NY 10024, USA

e-mail: iant@amnh.org

Summary - *Paleoanthropology's relationship with evolutionary theory has not been entirely happy. The anatomists who dominated paleoanthropology for its first century had little interest in biological diversity and its causes, or in hominins' place in that diversity, or in the rules and principles of zoological nomenclature – which they basically ignored entirely. When, as the twentieth century passed its midpoint, Ernst Mayr introduced theory to paleoanthropology in the form of the gradualist Modern Evolutionary Synthesis (in its most hardened form), he shocked students of human evolution not only into a strictly linear evolutionary mindset, but into a taxonomic minimalism that would for years obscure the signal of phylogenetic diversity and vigorous evolutionary experimentation among hominins that was starting to emerge from a rapidly enlarging hominin fossil record. Subsequently, the notion of episodic as opposed to gradualist evolution re-established phylogenies as typically branching, and species as bounded entities with births, histories, and deaths; but the implications of this revised perspective were widely neglected by paleoanthropologists, who continued to reflexively cram diverse new morphologies into existing taxonomic pigeonholes. For Pleistocene hominins, the effective systematic algorithm became, “if it isn't Australopithecus, it must be Homo” (or vice versa), thereby turning both taxa into wastebaskets. The recent development of the “Extended Evolutionary Synthesis” has only exacerbated the resulting caricature of phylogenetic structure within Homininae, by offering developmental/phenotypic plasticity as an excuse for associating wildly differing morphologies within the same taxon. Homo erectus has been a favorite victim of this foible. Biological species are indeed morphologically variable. But they are only variable within limits; and until we stop brushing diverse morphologies under the rug of developmental plasticity, paleoanthropology will remain at a major impasse.*

Keywords - *Paleoanthropology, Homininae, Evolutionary theory, Systematics, Taxonomy, Modern Evolutionary Synthesis, Extended Synthesis.*

Introduction

Paleoanthropology has from the beginning ploughed its own very distinctive scientific furrow. Whereas other branches of paleontology emerged in the early nineteenth century from geology and comparative anatomy, paleoanthropology developed later in the century in a rather haphazard way, as antiquarians, archaeologists, and others sent the human fossils they found to physicians and human anatomists for study. In one sense, of course, this was entirely reasonable. After all, nobody knew the human skeleton better than the anatomists; and for at

least the first quarter-century of its existence paleoanthropology had at its disposal only the bones of early modern humans and the broadly similar Neanderthals. But it did mean that from its earliest beginnings paleoanthropology was firmly insulated from the rest of evolutionary biology. And, perhaps most importantly from the perspective of its later repercussions, this isolation meant that the study of the human fossil record was initially shielded from developing ideas about evolution itself.

At first glance this might appear a little surprising, since it was early paleontologists, observers of the fossil record, who had first articulated

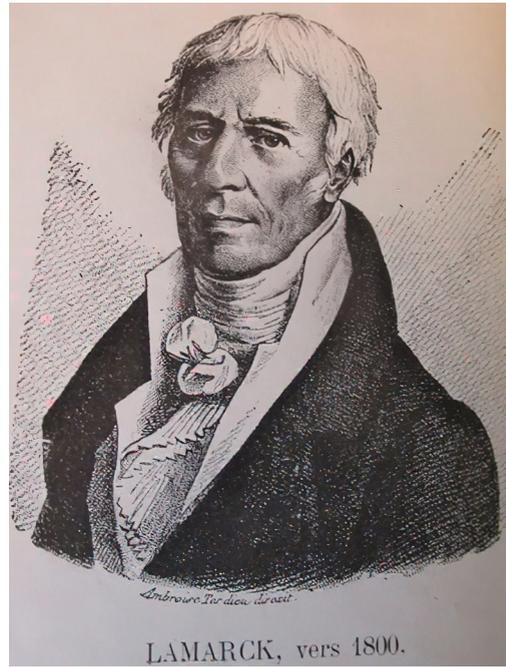
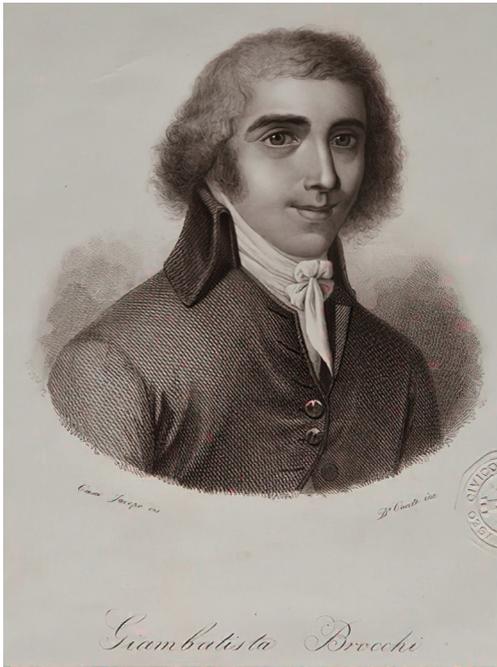


Fig. 1 – The early nineteenth originators of the two concepts that underwrite our understanding of evolutionary patterns today: Jean-Baptiste Lamarck (right), who proposed that lineages of organisms transform over time; and Giambattista Brocchi (left), who observed that species have finite lives in the fossil record, and deaths via extinction. Brocchi portrait courtesy of Stefano Dominici, Lamarck courtesy of Dave Bergman.

the two basic notions that underpin our understanding of evolution today: namely, that morphological change can accumulate within lineages over time (Lamarck 1809, Fig.1), and that species have births via splitting, finite lives as themselves, and deaths via extinction (Brocchi 1814, Fig 1). Yet even Charles Darwin's close associate Thomas Henry Huxley, an energetic proselytizer for evolution who was the first to realize that birds had evolved from dinosaurs, and whose 1863 book *Man's Place in Nature* was foundational to anglophone paleoanthropology, could not bring himself to apply evolutionary principles to human fossils. Instead of viewing the odd-looking Neanderthal fossil that had been discovered in Germany six years earlier in evolutionary context, Huxley tied himself into knots arguing that the Neanderthal was nothing more than an ancient and particularly brutish member of our own species, *Homo sapiens* (Huxley 1863).

Darwin's own *Descent of Man* (Darwin 1871) followed a broadly similar trajectory, at least to the extent that its author was willing to speculate about hypothetical human ancestors while scrupulously avoiding any discussion of fossils that might be germane to that ancestry. In the entire two volumes of the *Descent*, the one and only reference to the Neanderthal fossil merely observed that it showed that ancient humans could have big brains. This reluctance to integrate abstract evolutionary principles with the material human fossil record lingered with some tenacity. Thus, the early twentieth century's most widely read anglophone review of the human fossil record, Arthur Keith's *The Antiquity of Man* (Keith 1915), respected its title to the extent that it delved quite deeply into geological and archaeological sequences. But it contained nothing about natural selection, evolutionary process, or evolutionary patterns.

By the time Keith's volume appeared, Huxley's successors were prepared to accept diversity in the human fossil record. And indeed, Marcellin Boule had by then already made his Herculean attempt to portray the Neanderthals as creatures that were unlike modern humans as possible (Boule 1911-13). But another equally idiosyncratic and pernicious tendency had by that point replaced the denial of diversity: the misuse of zoological nomenclature. Paleontologists in other fields had long recognized that zoological names, and the Linnean hierarchy within which they were ranged, existed in some way to reflect the phylogenies that underpinned the order clearly observable in nature. And they acknowledged that supraspecific names were there to reflect the nested sets of organisms that systematists and paleontologists recognized on the basis of their morphologies. They also recognized that, while the genus/species binomen played an unusual role at the most fundamental level of this hierarchy, it was nonetheless an integral part of it.

Perhaps unsurprisingly, the anatomists did not share this perspective. After all, instead of trying to make sense of the riotous diversity of nature, they were fixated on one single species and on the minutiae of variation within it. Emancipated by this intense central focus from any perceived need to consider diversity, the paleoanthropologists were consequently free to use zoological names in any way they wanted. Which, apparently by analogy with the family and given names they themselves possessed, was basically as convenient tags to identify individual fossils. New hominin genus and species names were accordingly coined and thrown around with reckless abandon, so that by the middle of the twentieth century a dozen different genus names were in regular use for a limited number of fossils that are all subsumed today within the genus *Homo* (Tab. 1), with many more species names to boot. The result, of course, was to endow the still relatively poorly known human fossil record with a spurious appearance of great diversity. Franz Weidenreich, the highly respected anatomist and describer of the Weimar-Ehringsdorf and Zhoukoudian hominin fossils, described the situation very neatly when he was quoted as saying: "it always was and still is the custom to give generic

Tab. 1 – Genus names (with type species) that were in common use before World War II for the relatively few fossils then known that are assigned to genus *Homo* today.

<i>Pithecanthropus erectus</i>
<i>Meganthropus palaeojavanicus</i>
<i>Sinanthropus pekinensis</i>
<i>Atlantropus mauritanicus</i>
<i>Palaeoanthropus palestinensis</i>
<i>Palaeoanthropus heidelbergensis</i>
<i>Protanthropus neanderthalensis</i>
<i>Cyphanthropus rhodesiensis</i>
<i>Javanthropus soloensis</i>
<i>Telanthropus capensis</i>
<i>Africanthropus helmei</i>
<i>Homo spelaeus</i>

and specific names to each new type without much concern for the kind of relationship to other types formerly known" (Mayr 1950, p. 109).

As a result of its exceptionalist foibles, pre-World War II research in paleoanthropology had a distinctly different flavor from that in the evolutionary sciences in general. But practitioners of all branches of paleontology nonetheless shared one fundamental similarity: their analyses of the fossils to hand were based on "expert judgment." Everyone had his or her own story to tell, and the credibility of each story was conferred by the reputation, seniority, access to fossils, and sometimes the chutzpah of the storyteller, rather than by the restability or robustness of the story itself. Perceptions were always subjective, and often arbitrary. Hypotheses were not couched in testable terms, and their acceptance depended on the authority of their proponents. This was not a way of doing science that could endure in the long term, but it showed surprising durability. And for as long as it persisted, it papered over the fundamental procedural differences between paleoanthropology and the rest of paleontology.

The Modern Evolutionary Synthesis

Charles Darwin published his (and Alfred Russel Wallace's) notion of evolution by natural selection in his classic work *On the Origin of Species* (Darwin 1859). Following an initial uproar, the twin tenets that all life on Earth is united by common ancestry, and that the nested pattern of resemblances among organisms is due to "descent with modification," were remarkably rapidly accepted by most biologists as well as a large sector of the public. That rapidity is entirely understandable, for the idea that all life forms are related by descent is still our only hypothesis pertaining to the origin of natural variety that actually predicts what we see out there – and that reliably continues to do so, at the finer and finer levels of resolution that rapidly advancing technologies are making possible. What proved to be a harder sell, at least in the shorter term, was Darwin's choice for the driver of modification.

That choice was, of course, natural selection, whereby individuals with favorable heritable characteristics reproduced more successfully than their less well-endowed conspecifics, leading to the slow modification of each lineage of organisms as the generations passed. One of the larger problems that Darwin faced in convincing his audience that natural selection was what drove evolution was the lack of any convincing mechanism for heredity, the transmission of those favorable features from parent to offspring on which the process depended. Darwin was very well informed about animal and plant breeding, and he knew that biological heredity was real; but he had no clue about how that heredity worked. His espousal of the "pangenesis" notion, which held that the body's cells and tissues gave off "gemmules" that somehow accumulated in the reproductive organs, was no more than a guess: a mere placeholder that allowed him to complete his larger theory of evolution. Pangenesis, moreover, was not the only game in town: by the end of the nineteenth century, there were by one count as many as 30 different theories of heredity in circulation. This background makes it readily comprehensible that natural selection would begin to find widespread

favor as an evolutionary mechanism only once the heredity issue had been settled.

Back in 1866 the Czech cleric Gregor Mendel had proposed a theory of hybridity to which many now trace the origin of the modern science of genetics (though see Olby 1979; Kampourakis 2017). Things began to change only in 1900, when the basics of what we know today as Mendelian genetics were independently rediscovered in three European laboratories. Focusing on the expression of traits that were discrete (i.e., tall or short), researchers determined that the units of heredity were both discrete and paired (one from each parent), and that those that specified different traits were passed along independently of each other. Each unit of a pair (of what are now known as "alleles") retained its identity, and was passed intact from one generation to the next, even where a "dominant" form might mask the effects of its "recessive" twin in the phenotype (the physical appearance of the individual). The origin of the modern science of genetics is thus generally dated to that eventful year of 1900 when the discreteness of genes was established, although the term "genetics" itself dates only from 1905, and the word "gene" was not introduced for the unit of heredity until 1909. A key term that emerged very early on in the lexicon of genetics, and that remains central to it, was "mutation." This label had originated in the context of the distinctive new plant varieties that had long been known on occasion to arise spontaneously; but once Mendelian genetics came on the scene, it rapidly came to refer to the changes in the genes that underlay such "sports of nature."

Early researchers had stumbled over the Mendelian principles in search of answers to a range of different questions; but genetics as a science began to take on a more distinctly focused form when the Mendelian perspective was combined with the newly developed chromosomal theory of inheritance. Things moved fast, and the first map of genes along the chromosomes of the fruit fly *Drosophila* was completed in 1913 in the Columbia University (New York) laboratory of Thomas Hunt Morgan (Sturtevant 1913).

Two years later, the same laboratory revealed that at least 25 different genes were responsible for determining eye color in those fruit flies (Morgan et al. 1915): simple Mendelian inheritance was, it was turning out, a comparative rarity. Simultaneously, it was becoming realized that the environment in which an individual was raised could affect the expression of its underlying genes. The upshot was that, while everyone could agree that the rapidly developing science of genetics was somehow meshing well with Darwinian ideas of evolution, not everyone agreed how.

Accordingly, the first two decades of the twentieth century were a time of extraordinary hyperactivity for the nascent sciences of heredity and evolutionary biology, and almost everyone had his or her own theory about how inheritance and evolution worked, both at the genetic level and at the level of evolutionary change over time. Mutationists embraced the “saltationist” view which held that new species appear rapidly, through discontinuous transmutation. Darwinians, in contrast, held that change was slow, as selection within an existing spectrum of variation led to gradual long-term transformation. “Biometricians” noted that numerous genes appeared to be involved in determining continuously varying traits such as height or weight. Others thought that “mutation pressure” determined the rate and direction of change. Ideas of “soft” or “blending” inheritance continued to prove tenacious. And so on.

Things began to shake out when quantitative modelers began trying to integrate the empirical results that were coming in from all sides. Most notably, in 1918 the English quantitative geneticist R. A. Fisher published his “infinitesimal model,” whereby continuously varying physical characteristics – i.e., most of them – are determined by multiple genes, each of which makes a smaller relative contribution as numbers increase; and which between them, in conjunction with environmental influences, will produce a “continuous, normally distributed phenotype in the population.” This view did not exclude what we now view as Mendelian inheritance in the relatively few discontinuous traits known to

exist, but it did present a quantitation of the within-population variation on which Darwinian natural selection worked, and integrated it with a mechanism for the transmission of the hereditary information.

In retrospect Fisher’s analysis appears as a significant turning point that allowed a gradual convergence to begin among the systematists, geneticists, comparative anatomists, paleontologists, developmental biologists, and others whose work intersected with evolutionary science. At the time, though, it didn’t necessarily look that way; for there was plenty of mutual incomprehension to overcome, especially between the experimentalists and the empiricists. As the paleontologist George Gaylord Simpson eloquently put it, looking back from the vantage point of 1944:

Not long ago, paleontologists felt that a geneticist was someone who shut himself in a room, pulled down the shades, watched small flies disporting themselves in milk bottles, and thought that he was studying nature. A pursuit so removed from the realities of life, they said, had no significance for the true biologist. On the other hand, the geneticists said that paleontology had no further contributions to make to biology, that its only point had been the completed demonstration of the truth of evolution, and that it was a subject too purely descriptive to merit the name “science.” The paleontologist, they believed, is like a man who undertakes to study the principles of the internal combustion engine by standing on a street corner and watching the motor cars whiz by (Simpson 1944, p. xv-xvi).

Nonetheless, over the two decades following Fisher’s seminal contribution there emerged what became known as the “Modern Evolutionary Synthesis” (Huxley 1942), which integrated Darwinian ideas of natural selection with changing frequencies of genes in populations, and which brought specialists of very diverse kinds together into the nascent field of evolutionary biology. Perhaps the most compelling metaphor of the period was the statistician Sewall Wright’s

(1932) notion of the “adaptive landscape,” with its analogy to a topographic map in which the most viable (fittest) combinations of alleles (genotypes) clustered on the hilltops, while the less fit genotypes were scattered in the valleys between. Natural selection worked to keep the hilltops as crowded and the valleys as sparsely populated as possible, even as environmental change shifted the underlying topography. This image of the adaptive landscape very cogently married the ideas of natural selection and gene frequency change. And by catching the imagination of many, it set the scene for the full-blown development of the Modern Evolutionary Synthesis (hereafter, “the Synthesis”) as expressed not only in Huxley’s book, but in the approximately coeval and equally compelling presentations of three New York scientists with very different foci: the geneticist **Theodosius Dobzhansky** (1937), the ornithologist and systematist **Ernst Mayr** (1942), and the vertebrate paleontologist **George Simpson** (1944).

Although necessarily nuanced in its earlier manifestations, the Synthesis rapidly “hardened,” as the paleontologist **Stephen J. Gould** (1983) elegantly put it, into a firmly reductionist dogma whereby the evolutionary process consisted essentially of the gradual within-lineage accumulation of small genetic mutations and recombinations over vast periods of time. That slow accretion of changes over the generations took place principally under the control of natural selection, as individuals with superior heritable features out-reproduced their less favored conspecifics. Over long stretches of time larger-scale effects would result from the continuous accumulation of such minor changes, ultimately to produce higher-level phenomena such as the emergence of new species and the occupation of new ecological zones. By the mid-1940s, most anglophone adherents of the new science of evolutionary biology had come together to agree on these general principles. Even the paleontologists concurred, in a testament to the reductionist attractions of a Synthesis that had substantially short-changed them by relegating their basic unit of analysis, the species, to an evanescent entity that inexorably evolved itself out of existence.

The Synthesis and Paleoanthropology

The years following the end of World War II saw a generational change in paleoanthropology, as the prewar cohort of traditional anatomists and physical anthropologists began to age out of the profession, ultimately to be replaced largely by adherents of what was to become the “New Physical Anthropology.” This term was invented in 1951 by the physical anthropologist **Sherwood Washburn** (at the time a junior Columbia University colleague of **Theodosius Dobzhansky**, the most generally influential of the architects of the Synthesis), in the context of a clarion call for biological anthropology to switch away from the fusty old anatomical traditions of measurement and classification, and to embrace being a multidisciplinary and forward-looking science focusing on the mechanisms and processes involved in evolutionary change. Washburn’s appeal was hugely effective; and its timing was clearly far from coincidental, because it was made the year after what was, unquestionably, the most formative single intellectual event in the twentieth-century history of paleoanthropology.

In 1950, Long Island’s prestigious Cold Spring Harbor Biological Laboratory (CSHBL) convened a conference on *The Origin and Evolution of Man* that was attended by the leading figures in American evolutionary biology. The most resonant of the many presentations was made by the ornithologist **Ernst Mayr** (1950), identified earlier as one of the leading lights of the Synthesis. Mayr took as his theme “Taxonomic Categories in Fossil Hominids,” an issue that he undiplomatically positioned within the most hardened possible interpretation of the Synthesis. Bluntly – and entirely correctly – Mayr informed the paleoanthropologists in the CSHBL audience that, because of their “very intense occupation with only a very small fraction of the animal kingdom,” they had adopted “systematic standards that differed “greatly from those applied in other fields of zoology.” This, Mayr continued, had led to an unfortunate “attempt to express every difference

of morphology, even the slightest of them, by a different name” (Mayr 1950, p.109). In these words, Mayr peremptorily dismissed almost all of the many names available for hominin fossils (Tab. 1), declaring that the diversity implied by this forest of generic nomina was entirely illusory. In contrast, he insisted that the entire known hominin (to him, hominid) fossil record contained only three species. What is more, all three belonged to the single genus *Homo*, and all represented sections of one single, gradually evolving, and time-transgressive lineage. *Homo transvaalensis* (what we would now today refer to as the gracile australopiths) transformed insensibly into *Homo erectus*, which in turn gradually became *Homo sapiens* (via the Neanderthals). And that was it. Any morphological discontinuities an observer might have perceived in this sequence were no more than artifacts of an imperfect fossil record: in the dimension of time, the three species had possessed no morphological or behavioral boundaries. Which was, Mayr sonorously continued, entirely inevitable, because “Man has specialized in despecialization ... if the single species man occupies successfully all the niches that are open for a *Homo*-like creature, it is obvious that he cannot speciate” (Mayr 1950, p.116).

Mayr’s audience reacted strongly to this direct assault – and not because it was hearing this rigorously linear and gradualist dogma from a man who was already developing a reputation as an expert on speciation and the origin of new lineages. Instead, the strength of the reaction reflected the fact that, by 1950, the cracks in the existing paleoanthropological edifice were already in plain sight. It is clear, for example, that some of the older generation of paleoanthropologists were already at least subliminally aware that they had scant theoretical justification for their nomenclatural extravagances, and that they had been guilty of neglecting the wider evolutionary implications of their systematic follies. This had certainly been true of the then very recently deceased Franz Weidenreich, who had finished his career at the American Museum of Natural History, the academic home of both Ernst Mayr and George Simpson (see the

recollections quoted in Tattersall 2009). And their younger colleagues (including Washburn) had already been primed by their association with Dobzhansky and others to embrace the new perspective. Change was by then in the air, awaiting catalysis; and it was Mayr’s broadside that proved to be the catalyst, with immediate and lasting impact.

On the other hand, if Mayr’s intention had been to shock the paleoanthropological profession into bringing its systematic standards into line with those employed by other paleontologists and systematists, he was surely disappointed. For the presumably unintended effect of his upbraiding was to cause paleoanthropologists of all inclinations (not only the Old Guard at whom he had taken direct aim, but the Young Turks too) to shy away from systematics entirely. Each group had its own reasons for doing this, but the effect was identical across the board. For at least a decade, paleoanthropologists of all stripes shunned zoological nomina entirely. Mayr had urged, specifically in the case of the South African australopiths, that “until a real taxonomic distinction has been established ... it would be safer and more scientific to refer [to them] by vernacular names” (Mayr 1950, p.113); and paleoanthropologists not only welcomed this advice but broadened it to embrace the entire human fossil record. Hominin phylogenetic trees lost their branches, and instead became agglomerations of bubbles and broad arrows within which informal designations such as “Swanscombe,” and “Starosele” floated in varying proximities. Practically no anglophone paleoanthropologists wanted to go near a zoological name.

Almost the only dissenting voice was that of the South African paleoanthropologist John Robinson, whose ox Mayr had specifically gored. Robinson very reasonably drew attention to the bounteous evidence offered by the South African australopiths that multiple lineages had indeed existed in the hominin fossil record (Robinson 1953), a point that Mayr rapidly, if grudgingly, conceded (Mayr 1953). Nonetheless, such was the power of Mayr’s onslaught that most anglophone paleoanthropologists were happy to

drop the now-tendentious matter of taxonomy entirely, and to content themselves instead both with those vernacular names, and with the lack of phylogenetic precision that came along with them. This abandonment of taxonomy and phylogenetic accuracy came, naturally enough, at a major long-term cost. It resulted in an entrenched taxonomic minimalism, a reluctance by paleoanthropologists to embrace as many categories as were needed to express the richness of the hominin fossil record and the complexities of descent it encodes. The hominin fossil record has expanded out of recognition since Mayr handed down his graven tablets from the Cold Spring Harbor mountaintop; but in obeisance to his strictures, and despite the wealth of new fossils and morphologies available, almost three-quarters of a century later paleoanthropologists remain extremely reluctant to create new categories to accommodate all this novelty. The result is that Homininae has become a small jumble of wastebasket taxa as paleoanthropologists have energetically shoehorned new morphologies into old species, in the process caricaturing both (see Tattersall 2017).

None of this is to say that the results of Mayr's intervention in paleoanthropology were entirely negative. That was because the Synthesis was not fundamentally about taxonomy, but about biology and evolutionary process. And even as they turned their backs on systematics, the postwar generation of paleoanthropologists willingly embraced the many positive things that the Synthesis had to offer. This was done largely under the influence of Theodosius Dobzhansky, who had offered paleoanthropologists his gradualist and unilinear perspective on human evolution as early as 1944, and who dedicated a major book to the subject in 1962. Unlike the traditional anatomists, the advocates of the Synthesis thought in terms of populations and of ancient demographics. They thought in terms of changing environments, and of function, and of individuals striving to achieve reproductive success in challenging circumstances. More than anyone before them, they consciously emphasized how intricately complex and interactive the

extinct worlds of the past had been. Some earlier paleoanthropologists such as Franz Weidenreich at Zhoukoudian, and Raymond Dart most famously at Makapansgat, had sought to bring their ancient subjects to life in particular respects; but under the sway of the Synthesis multifactorial explanatory narrative took center stage, and paleoanthropological analyses such as those of the Neanderthals by Washburn's student Clark Howell (1951, 1952, 1957) routinely assumed a freshness and a three-dimensionality that had generally been lacking under the old "measure and classify" regime.

New zoological names returned to the fore in 1964, in a curious and temporary reversal when Louis Leakey and two illustrious colleagues (L. Leakey et al. 1964) named the new species *Homo habilis* from the earliest exposures in Tanzania's Olduvai Gorge. Unlike his paleoanthropological colleagues, the unconventional Leakey was always ready to name a new species of anything at the drop of a hat; and, deeply under the sway of the then-pervasive idea of "Man the toolmaker" (i.e., that the making of tools was the hallmark of the genus *Homo*) he was on a single-minded mission to find the remains of the hominin that had made the crude stone tools that had for years been turning up in the lowest levels of the Gorge. He was a bit disappointed by the first candidate fossil, found in 1959. This was the hyper-robust australopith he called *Zinjanthropus boisei* (L. Leakey 1959); and even he could see that it was a bit too specialized to be considered ancestral to modern humans. Consequently, he was greatly relieved when the remains of a more gracile and generalized hominin soon turned up in Olduvai deposits of approximately the same age (L. Leakey 1961). Here was his toolmaker; and Leakey clung to the idea that it was an early member of *Homo* even after the oldest of the fossils came in with a mind-boggling potassium-argon age (L. Leakey et al. 1961) of 1.8 million years (myr), three times what he had informally estimated.

Many at the time felt that the holotype mandible of *Homo habilis* was not appreciably different from its counterparts among the gracile South African australopiths; but when a very

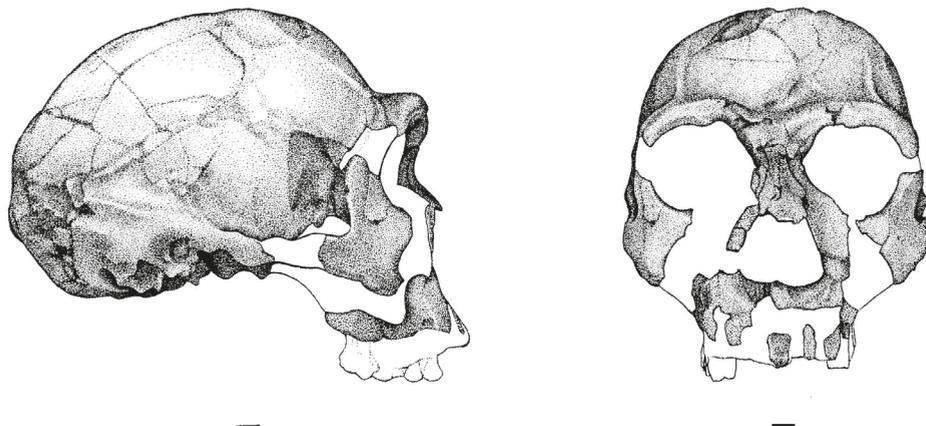


Fig. 2 – Front and side views of the 1.63-million-year-old East Turkana fossil KNM-ER 3733, the best-preserved example of an adult *Homo ergaster* cranium. Drawing by Don McGranaghan; centimeter scales.

fragmentary Olduvai braincase was estimated to have an endocranial volume (a proxy for brain size) of some 680 ml, versus the australopith mean of around 450 ml (modern humans average 1,330 ml: all averages quoted here are from Holloway et al. 2004), he felt he had morphological justification for placing the whole gracile Olduvai assemblage in the genus *Homo* (L. Leakey et al. 1964), even though the higher brain volume still lay below the “cerebral Rubicon” of 750 ml. that Arthur Keith (1931) had established for *Homo* a quarter-century earlier. Leakey made this judgment, of course, in the service of what we now know to be a major misconception (that stone toolmaking was the foundational human quality, and the hallmark of the genus *Homo*); but it was fundamental to two trends that have marred paleoanthropology ever since. One of those twin unfortunate tendencies is the dichotomizing of virtually all early Pleistocene hominins into *Australopithecus* or *Homo*; the other is the frenetic search for the “earliest *Homo*,” at the expense of seeking phylogenetic pattern in the human fossil record.

After much initial grumbling (see account in Tattersall 2009), *Homo habilis* became generally accepted among anglophone paleoanthropologists as an appropriate designation for the gracile Olduvai materials, especially after Louis’s son Richard had found, to the east of Kenya’s Lake

Turkana, a fragmentary and edentulous 1.9 myr-old cranium with a cranial volume of around 800 ml (R.E.F. Leakey 1972). The specimen concerned was the KNM-ER 1470 fossil that is now generally referred to *H. rudolfensis* (see Wood 1999), but that was seen at the time as settling the taxonomic argument in favor of *H. habilis*. Notably, though, Richard soon parted company from his father (yet again). He tacked sharply in the other direction, and took the general reluctance to introduce new species names into paleoanthropology to a ludicrous extreme by banning the allocation, to any species whatever, of any hominin fossil from East Turkana that was suspected of membership in the genus *Homo*. The Turkana literature consequently became saturated with a confusing welter of hominins referred to just as “*Homo* sp.”

Eventually Richard relaxed the ban, just in time to allow a remarkably complete 1.6 myr-old adolescent hominin skeleton found at Nariokotome, a site near the western shore of Lake Turkana (F. Brown et al. 1985, Fig. 2), to be classified as “early African *H. erectus*.” This designation (derived directly from Mayr’s characterization of *Homo erectus* as “the hominid in the middle”) was chosen despite the plainly evident fact that, beyond a broadly similar cranial capacity of around 880 ml, the Nariokotome

skull bore little resemblance to the much younger (>700,000-year-old) holotype skullcap of *H. erectus* from Java. Informally known as the “Nariokotome Boy,” the new skeleton (Fig. 2), had close to modern bodily proportions, showing long legs, relatively short arms, and (relative to australopiths) a narrow pelvis; and nowadays many classify it as *H. ergaster*. This is a name originally given by the interlopers Colin Groves and Vratja Mazak (1975) to a 1.5 myr-old mandible from East Turkana, and the species concerned is best exemplified in fully adult form by the reasonably complete KNM-ER 3733 cranium (Fig. 2). By the 1980s, then, paleoanthropology had begun to throw off its Mayr-induced absolute aversion to zoological names. But it retained its minimalist stance, even as it veered back towards the prewar arbitrariness that Franz Weidenreich had described so well. And it was doing so in an entirely ad-hoc way, unguided by any coherent theoretical framework or expectations.

Post-Synthesis Developments

Although George Simpson (1944) had very stylishly brought his discipline of paleontology into the fold of the Synthesis in his *Tempo and Mode in Evolution*, the formulation of evolution as a matter of gradual lineage transformation had, as noted, severely handicapped paleontologists by depriving the fossil species, their most fundamental unit of analysis, of an objective existence. Species might appear to have reasonably well-defined boundaries in space, where the systematists dwelled; but the Synthesis saw them as unbounded in time, gradually and inexorably evolving themselves into something else. For paleontologists, species as thus conceived would be impossible to define or to recognize, even in principle. Even worse for the students of the fossil record (who had, after all, got the whole evolutionary ball rolling in the first place), the Synthesis had relegated paleontology to the humble clerical task of documenting and classifying the results of evolution, while its mechanisms and grand patterns lay in the purview of

the geneticists and systematists. As a result, it is hardly surprising that the first major attack on the Synthesis came from the direction of paleontology. In 1972 the invertebrate paleontologists Niles Eldredge and Stephen Jay Gould pointed out (Eldredge and Gould 1972) what many paleontologists had known all along, which was that most fossil species appeared rather abruptly in the fossil record, lingered for varying lengths of time, and then disappeared, to be replaced as often as not by a close relative. Far from being gradual, as predicted by the Synthesis, evolutionary change has accumulated in fits and starts, as new species came on to the environmental stage, competed for ecological space, gave rise to descendant species in the short-term process of speciation, and eventually became extinct, with or without progeny. As visualized in a phylogenetic diagram, this process produced a more or less luxuriantly branching bush of taxa, in sharp contrast to the ladder-like structure predicted by the Synthesis.

In the new view, whether or not a species succeeded in the long term would often have depended much less on its innate qualities (as honed by traditional natural selection) than on whom it happened to be competing with, and under what environmental conditions. Changes in external conditions that had no relation whatever to excellence of adaptation were seen as key overall influencers of evolutionary patterns, and internal processes *within* species took on a different role from before, as stabilizing influences. Eldredge and Gould (1972) named the process of lineage splitting, followed by varying periods of stasis, “punctuated equilibria,” and they contrasted it with the transformational “phyletic gradualism” of the Synthesis. What’s more, they suggested that punctuated equilibria provided a much better fit than gradualism to what most paleontologists actually saw in the fossil record.

Under punctuated equilibria, species ceased to inexorably evolve themselves out of existence, and instead regained their importance as individualized actors and interactors in the evolutionary play. Similarly, overall patterns of evolutionary change came to be seen as more deeply affected by external forces than by the intrinsic excellence

of the individuals who reproductively competed within those species. After all, in the larger scheme of things, of what use is it to be the most excellently adapted member of your population in some aspect or another, if your entire species is being outcompeted into extinction, or if it is being made unviable by local environmental change? Darwinian natural selection might still, of course, be expected to occur under conditions where the putative selective agent was very close to critical aspects of reproduction or survival (think large testes in promiscuous chimpanzees, or lactase persistence in cattle-herding human populations). But in the light of punctuated equilibria, natural selection (which is a mathematical certainty in any population in which more individuals are born than survive to reproduce) can begin to be seen not so much as an active agent of inevitable change, but as a principally stabilizing influence that acts mainly to trim off the less viable extremes in the normal curves of character distributions produced by Ronald Fisher's infinitesimal model of gene behavior. By promoting homeostasis in this way, natural selection's main large-scale effect is to keep entire populations as fit as possible (amid fluctuating environments). And then again, beware in an uncertain world of excessively tight adaptation to any specific environment: extinction rates have typically been far higher among the stenotopes (specialists) that are very highly honed to their environments, than they are among eurytopes (generalists) such as hominins (Eldredge 1979). Further, the homeostatic perspective fit well not only with the reality, established early on, that most genes are pleiotropic (affecting many characters) while most characters are polygenic (affected by many genes), but also with the obvious although frequently overlooked fact that strictly Darwinian natural selection can only work on entire individuals, which must necessarily succeed or fail as the sum of their parts. Being the keenest-eyed of your group may not help you much in the long run, if you are also the slowest.

In long retrospect, the advent of punctuated equilibria looks like a simple return to reason. At the time, though, even as it felt like a major

conceptual leap forward to some of us, it provoked a strong adverse reaction among others. Still, at the very least its implications should have come as a wake-up call to those paleoanthropologists who, under the sway of the New Physical Anthropology and Mayrian linearity, were increasingly focusing on the "evolution of the brain," or the "evolution of the gut," or "the evolution of the foot," as if those systems had independent existences whose modification could be independently traced over vast tracts of time. Which was, of course, very clearly not the case: all anatomical systems are embedded in individuals and in the species to which those individuals belong; and each one is inextricably interlinked with all the other properties of the organism involved. For those who were willing to see it, by the mid-1970s it was already blindingly evident that without a strong systematic framework, and without knowing how the various states of the features of interest were distributed among the taxa in a phylogeny, it was simply not possible to make proper sense of the changes in physical properties observed over time. Nonetheless, both the taxonomic minimalism that was Mayr's paleoanthropological legacy, and the traditional human anatomist's tendency to dismiss taxonomy as "merely arguing about names," proved highly durable. The tendency to proceed with paleoanthropological analysis without establishing an adequate phylogenetic structure lingered powerfully, and still casts a very long shadow.

Punctuated Equilibria and Systematics

Perhaps the single most salutary effect of the new punctuated equilibria perspective was to restore the identity of species as bounded units: entities with definable characteristics that invited phylogenetic analysis. And, coincidentally, the arrival of punctuated equilibria had broadly coincided with the advent of cladistics, the school of phylogenetic analysis that insisted that taxa should be linked on the basis of synapomorphy. Synapomorphies are derived characteristics

(or states of the same character) that are shared among two taxa (“derived” indicating departure from the common ancestral condition). Two pairs of related taxa united by one or more synapomorphies could, in their turn, be united using other shared common ancestral characters, and so on down the line to obtain a branching diagram that indicates the relationships by descent of all the members of the group under consideration. The resulting explicit statements of relationships by descent were known as “cladograms,” and they were scientific to the extent that they could be tested and potentially rejected by the addition of new characters or new taxa to the analysis. All species were treated as terminal, both living and extinct species being given identical treatment. There are, of course, two possible kinds of relationship by descent: that between two “sisters” uniquely descended from the same common ancestor, and that between an ancestor and its direct descendant. Cladograms do not attempt to distinguish between these because, while sister relationships are encoded in synapomorphies, the ancestor-descendant relationship is not directly testable as such (Tattersall and Eldredge 1977).

This systematic advance depended, naturally enough, on the fact that if it was to offer usable systematic characters, any species obviously needed to possess the finite morphological boundaries that phyletic gradualism had denied it. Punctuated equilibria had provided that. And in its turn, once such boundaries had been acknowledged by the punctuated equilibria model, the cladistic approach ensured that taxa could at least in principle be identified and grouped in an objective and testable way.

If less overtly, cladistics also offered a new mindset to paleontology. Under the Synthesis, species had essentially formed chains running through time, a perspective that had implied in turn that understanding evolutionary histories was not a great deal more than a matter of discovering fossils (Eldredge and Tattersall 1975). If, as Mayr’s model implied, a fossil’s historical place was a simple function of its chronological position, it followed that if you crawled over

enough outcrops, and collected enough well-dated fossils, the course of evolution would simply be revealed, much as the picture emerges in a jigsaw puzzle as the pieces drop into place. This belief in the magical properties of discovery was, indeed, what had implicitly permitted paleoanthropologists to skip the essential systematics stage when evaluating a fossil or a fossil assemblage, in favor of proceeding directly to the “more interesting” ecological and behavioral stuff. But if phylogenies were complex branching structures, as it was rapidly emerging during the 1970s they typically were, the story was entirely different. Phylogenies could not be directly discovered. Instead, they were a matter of careful analysis. Discovery of fossils was obviously important; but the accumulation of fossils was now seen by most paleontologists to be only the beginning of a much longer process: one that had to start with basic phylogenetic inquiry.

The advent of cladistics was thus as truly radical for systematics as that of punctuated equilibria had been for evolutionary theory, for it banished the expert judgment that had ruled for so long. If you wanted to demonstrate that two taxa were each other’s closest relative, you had to be able to show how they were exclusively linked by derived characters free of homoplasy (independent acquisition). Sadly, though, old habits die hard; and despite the compelling logic behind the approach, “cladist” is still sometimes used as a term of opprobrium in paleoanthropology. At the time, however, cladistic theory and procedures offered a welcome breath of fresh air to some of us; and, from the contemporary perspective, their most important contribution was to open the way for the quantitative computer-driven approaches (using mainly parsimony and maximum likelihood algorithms) that are nowadays used to generate and test phylogenetic trees. Making use of sometimes mind-bogglingly large data sets, such procedures are by now routinely employed in all areas of systematics, very occasionally also including paleoanthropology (e.g., Dembo et al. 2015).

Significantly, though, the quantitative methods that have been most eagerly adopted by

paleoanthropologists have tended to be such multivariate procedures as principal components analysis and geometrical morphometrics. Not only do these techniques not produce phylogenies, but they are not means of analyzing data and are rather ways of visualizing them. And, when one is dealing with fossils, the human eye/brain combination is in many cases probably at least as efficient at visualization as the shooting of vectors through multivariate space is. Of course, you do emerge from those quantitative exercises with a lot of numbers; but they are unlikely to mean much until you have been able to precisely situate the fossils you have quantified within a phylogeny.

Other quantitative visualization methods that have been widely used in paleoanthropology include the “virtual anthropology” techniques that involve scanning broken or distorted fossils, then disassembling and rejoining them on the computer screen with the option of 3-D printing the result. At least for research purposes, the technological ability to do this will soon have all but replaced the earlier, labor-intensive, and time-consuming process of manual fossil preparation and reconstruction; and it also permits the production of replicas without the wear-and-tear and risk of physical damage inherent in traditional preparation and molding-and-casting procedures. These advantages have, of course, been of huge benefit to paleoanthropology; but once you have your high-resolution reconstruction in your hands, you still require some way of analyzing it. And, even more importantly, you first need to have some way of accurately classifying it. This is a current weak point, because prior grouping of fossils into units of analysis (usually species) is normally obligatory; and such groupings are typically all over the map from one researcher to the next. Indeed, they usually involve informal groupings rather than species.

One reason for this is that the species is the one single level in the entire Linnean hierarchy that, even in principle, is not recognized on the basis of morphology; and there is no quantitative method I am aware of that claims to reliably allocate fossils to species. Regrettably, then, an unavoidable element of subjective judgement is

still involved in sorting fossil assemblages into these fundamental units; and although as a general rule of thumb species do tend to vary around fairly readily recognizable themes, there is probably a general tendency to underestimate their frequency in the fossil record (Tattersall 1996).

But species recognition difficulties are not the sole, or even the major, reason why paleoanthropologists so rarely use analytical methods to construct hominin genealogical trees. The principal difficulty with using widely available quantitative phylogenetic/analytical procedures in paleoanthropology is very likely that their use depends on the existence of extensive and reliable data matrices. Such data sets are relatively easily compiled when one is dealing with long-established taxa within which a lot of differentiation has occurred; but in paleoanthropology we are dealing with a recently evolved and very closely related group within which differentiation is often minimal, homoplasy is rampant, and variation is rife. What is more, we are looking at human evolution in such extremely fine grain that both reliably recognizing fossil species, and compiling large discrete data matrices, are supremely difficult tasks. To use quantitative phylogenetics you need well-defined and well-documented operational taxonomic units in addition to a solid data matrix, and the structuring of such units among the hominins is such a tricky issue that paleoanthropology has found it most convenient to avoid confronting it.

There is, moreover, another level of complication in paleoanthropology: one that is not only related to the very intensive level at which we scrutinize our data, but to the extremely close phylogenetic affiliations of the lineages under scrutiny. Genomic information at varying levels of resolution is now available on certain fossil hominins as far back as 400,000 years or so (Meyer et al. 2016); and it indicates not only that there were more lineages out there than we had guessed from the fossils alone (Reich et al. 2010), but that interbreeding was fairly routine among more recently differentiated lineages within the genus *Homo* (Villanea and Schreiber 2019). This appears to have been true even when the

lineages concerned (such as *Homo sapiens* and *H. neanderthalensis*) were clearly already established on independent evolutionary trajectories. In the instances we are able to recognize, such genetic interchange may have made minor differences to adaptability in the recipient lineages (e.g., Huerta-Sanchez et al. 2014); but long-term evolutionary outcomes were nonetheless broadly unaffected. There may well also, of course, have been some so far undetected reticulating expressions; and the wider message is obvious that there was a significant amount of lineage splitting, and probably of reticulation as well, within the genus *Homo* in the later part of the Pleistocene. Any of the very subtle signals that reflect those events in the recent hominin record will, however, likely not be easy to decipher.

Taxonomy of the Genus *Homo*

We saw earlier that by the middle 1980s mainstream paleoanthropologists (of whom Louis Leakey had never been one) were beginning to countenance the very occasional new species name for newly discovered hominin fossils, simply in response to the pressure of discovery. What remained largely taboo, though, was the proposal of new genus names, although by around the turn of the twenty-first century even this taboo had been violated in the case of a string of discoveries of very early putative hominins in the 7-3.5 myr bracket (*Ardipithecus*, *Sabellanthropus*, *Orrorin*, *Kenyanthropus*). In the case of more recent hominins, however, the old injunction remained. If a robust australopithecine fossil was found, in obedience to tradition it would duly be assigned to *Paranthropus*. It was, as it were, grandfathered in. Otherwise, however, the choice was essentially between *Australopithecus* and *Homo*. The implicit algorithm for Pleistocene hominins (especially using the older short chronology: Gradstein et al. 2004) became: "If it isn't *Australopithecus*, it must be *Homo* – or vice versa" (see Tattersall 2014 for more detailed discussion). In effect, the diagnosis to genus became one of exclusion, with little

attention paid to the morphological affinity that should have positively guided the determination.

The genus is, of course, a conceptually tricky taxonomic category. Living species define themselves, in the sense that they are the largest freely and effectively reproducing groups in nature: their members basically know who they are, and it is up to biologists to discover what it is that they know from all possible lines of evidence available, ranging from the reproductive, through the developmental, to the ecological. Genera, on the other hand, are the creation of taxonomists. They are necessarily monophyletic groups of species (i.e., including only the descendants of a particular common ancestor); but there is no rule that specifies how many species a genus should embrace. There is, perforce, a phylogenetic structure (a branching pattern) within every polyspecific genus; and how many branching events a given genus should embrace is essentially an arbitrary decision on the part of the taxonomist. And what is most remarkable, given this subjective/arbitrary element, is that there is on the whole so little argument about mammalian genera. Among mammals a genus may contain many species or only a few; but it will always have a *Gestalt* quality that is instantly recognizable and shared among its members. Why exactly this should almost invariably be the case – no matter how speciose the genus – when in evolution the tendency is to diversify, I do not know, if it is not that even sister clades will inevitably diversify along their own unique lines. But as a rule, all members of well-established genera share a basic *Bauplan* that is instantly recognizable, even when body sizes vary greatly. One genus does not grade into the next, and the exceptions are very few.

When Linnaeus named the genus *Homo* in 1758, its type and only species (apart from *Homo troglodytes*, an ape) was *Homo sapiens*, a very unusual, large-brained, globe-headed, microdont, tall and slender biped that, by definition, was and remains the standard by which membership in the human genus had, and has, to be measured. By the time Mayr traumatized paleoanthropology in 1950, only a couple of fossil species were

known that by most standards deserved inclusion in the genus: the large-brained and relatively recent *H. neanderthalensis*, and the rather older and smaller-brained *H. erectus* from Java and China. The three made a reasonably compact monophyletic assemblage, and even a *Gestalt* one, despite the significantly smaller brain of the Javan form – which was, nonetheless, comfortably larger than that of the australopiths (the early bipeds, known since 1925).

As we saw, Louis Leakey put the cat among the pigeons in 1964 when, along with Phillip Tobias and John Napier, he named the extraordinarily ancient and notably small-brained *Homo habilis*. Paleoanthropologists by that time had moved on somewhat from typology; but few had much experience in mammalian systematics, and despite some initial grumbling opinion eventually moved in Leakey's favor. The very small-brained (for *Homo*) and very australopith-like gracile Olduvai material became an accepted part of the *Homo* hypodigm. And once the morphological concept of *Homo* had been so dramatically broadened by this addition the sky was the limit, and fossils with very little similarity to *Homo sapiens* were crammed in. Each new addition expanded the boundaries of the human genus in some way, making it easier for new arrivals, however inappropriate, to qualify as well.

Over the years *Homo habilis* expanded well beyond Olduvai, to embrace a variety of mostly fragmentary fossils from various parts of southern and eastern Africa that were up to about 2.5 myr old. The miscellaneous nature of the assemblage eventually became sufficiently embarrassing for some anthropologists to start calling some of its members "*Homo* sp." once more. And then the floodgates opened. In 2004 an extremely diminutive skeleton (LB1) and other materials from the cave site of Liang Bua in the Indonesian island of Flores (P. Brown et al. 2004) were given the name *Homo floresiensis* (Fig. 3). The tiny LB1 individual (it had stood 106 cm tall, about the height of the small *Australopithecus afarensis* individual known as "Lucy") had bizarre body proportions, a small dentition like nothing ever seen before, and a brain volume of only 426 ml;

and it had lived less than 100,000 years ago. So strange was it, that many thought the skeleton pathological, a notion eventually refuted not only by the elimination of all candidate pathologies, but by the discovery of other, similar materials at another site. But the attribution to *Homo* has stuck: an attribution that could only ever have been arrived at by concluding (correctly) that it was not *Australopithecus*, in the context of the belief that those two options were the only ones available. Some >50,000-year-old bone fragments from a cave on the island of Luzon in the Philippines are similarly small, and it has been suggested that they may belong to a related form, *H. luzonensis* (Detroit et al. 2019).

A genus that could contain both *Homo sapiens* and the Flores hominin would already boggle the minds of most mammalian taxonomists; but more was to come. In 2015 the discovery was announced (Berger et al. 2015) of a trove of fossils belonging to another diminutive hominin species, in a limestone cave system adjacent to some of the most famous South African australopith sites. Though a bit taller than LB1, these new hominins were small, standing on average around 144 cm high; and they boasted brain volumes ranging from 465 to 610 ml, along with protrusive faces (Fig. 3) and many archaic postcranial features. Most observers guessed from the fossils' physical attributes that they were in the range of 1.5 to 2 myr old, and amazement prevailed when they were dated to only around 300,000 years ago (Dirks et al. 2017). And yet these archaic-looking creatures, too, were assigned to our own genus, as *H. naledi*. Once more, one can only conclude that the "if it isn't *Australopithecus*, it must be *Homo*" algorithm was at work. For indeed, the Rising Star hominins are not *Australopithecus*.

Something similar must also be said of the astonishing series of 1.8 myr-old hominin fossils discovered since 1992 at the site of Dmanisi, in the Republic of Georgia, in association with Oldowan (Mode 1: very archaic) stone tools. They are the earliest non-African hominins attested to by fossils (there are earlier archaeological intimations of hominins in Asia). By now,

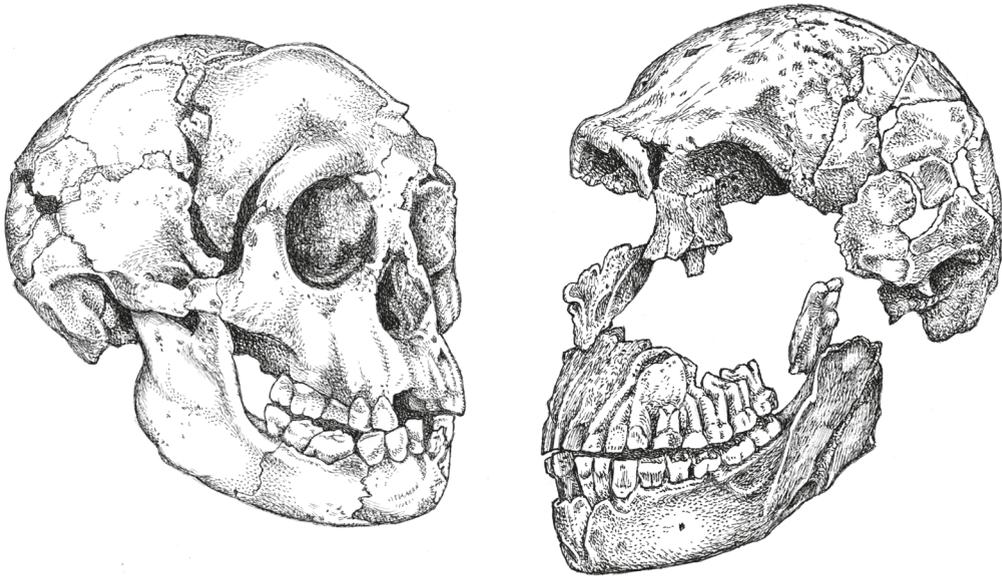


Fig. 3 – Skulls of *Homo floresiensis* (left), and of *H. naledi* (right). Drawn by Patricia Wynne; not to scale.

five skulls are known, three with associated postcranial materials; and they make up a very miscellaneous assemblage (see summary by Rightmire et al. 2006; see also Schwartz et al. 2014, and Tattersall 2015). Although assigned to *Homo* from the very start, the Dmanisi hominins have had a wild taxonomic ride at the species level (and below), one or more of them having at one time or another been assigned to *H. habilis*, *H. erectus*, *H. ergaster*, *H. georgicus*, and most recently (and as illegally as amusingly) to the sub-species *H. erectus ergaster georgicus* (Lordkipanidze et al. 2013). All five Dmanisi hominins are united by small brains in the 546-775 ml range; and the preserved postcranial elements indicate not only very modest stature but gait differences from modern humans (Lordkipanidze et al. 2007). The five crania present a variety of morphologies that has yet to be sorted out; but if there is one thing on which all can agree, it is that the last-found of the crania (D 4500, matched with the earlier-discovered mandible D 2600; together they are known as “Skull 5,” Fig. 4) is hugely distinctive. This is not the place to go into detail;

but if all the Dmanisi hominins can be crammed into the genus *Homo*, then virtually any hominin can be. Under these perversely ecumenical circumstances, there is no chance whatever of deriving any coherent morphological definition of the genus *Homo*, or of deriving phylogenetic structure from the vast array of morphologies that the genus now covers.

Still, at a time when paleoanthropology’s equivalent of the medieval quest for the Holy Grail seems to be the search for the most ancient possible representative of our genus, that may not be perceived as the point. Since Louis Leakey’s day, the epicenter of that search has moved from Tanzania to Kenya, and thence to Ethiopia, where the latest entrant in the “the earliest *Homo*” stakes is the partial hominin mandible identified as NME LD 350-1. This comes from the Afar site of Ledi-Geraru, which is dated to 2.8 myr (Villmoare et al. 2015). Ledi-Geraru is geographically close to the Hadar area, from which slightly older and slightly younger hominin fossils had already been recovered, and assigned to *Australopithecus*

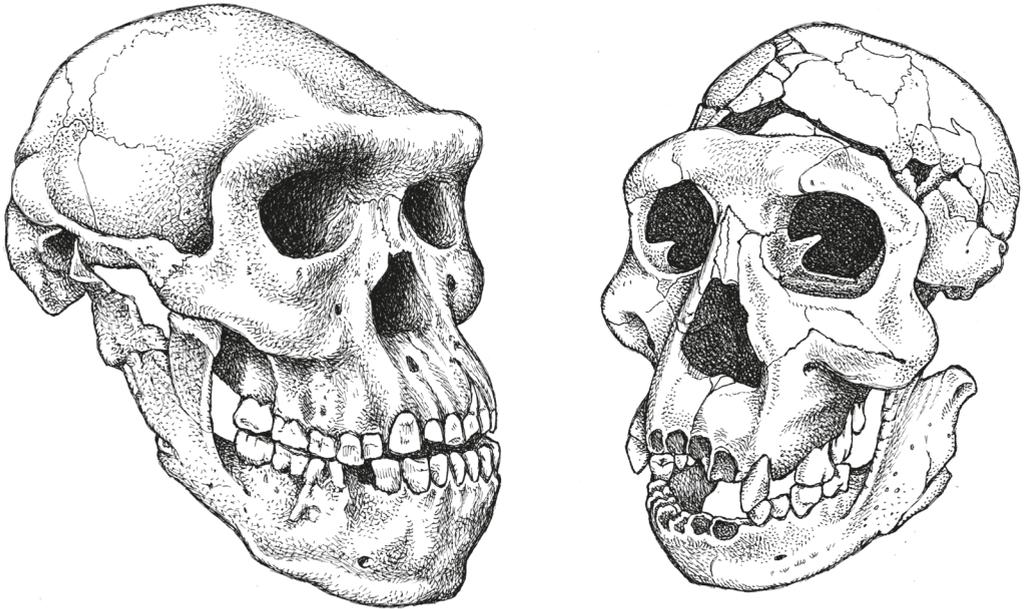


Fig. 4 – Two of the series of 1.8-million-year-old skulls from Dmanisi, Republic of Georgia. Left: D 2600/4500, “Skull 5.” Right: D 2700/2735, “Skull 3.” Despite its many unusual features Skull 5 has been eccentrically designated “*Homo erectus ergaster georgicus*” (Lordkipanidze et al. 2013). Drawn by Patricia Wynne; not to scale.

afarensis and *Homo* sp., respectively. Villmoare and colleagues reported that the LD 350-1 specimen not only matched smaller individuals of Hadar *Australopithecus afarensis* in size, but also shared various mandibular features with them. However, they also pointed to some dental differences that they felt “aligned” LD 350-1 with “early *Homo*,” in addition to noting some unique features in the new specimen. In a move that one can only attribute to the lingering influence of Ernst Mayr, the researchers concluded that Ledi-Geraru mandible sampled the gradual evolutionary transition that they hypothesized had occurred in the region from the older *A. afarensis* to the younger *Homo* (species unspecified). By arbitrarily assigning the chronologically intermediate Ledi-Geraru specimen to the human genus (as under Mayr’s rules they were entitled to do), they were able to claim the “earliest *Homo*” title. Of course, the “*Homo*” to which Villmoare and colleagues were comparing their new find already represented the genus at its most unattractively

bloated; and the comparison looks very different if it is made with the type species of the genus instead. Still, it nonetheless remains entirely possible that sufficient morphological justification exists for concluding that the Ledi-Geraru fossil belongs to a taxon distinct from *A. afarensis*; and it is even conceivable that the taxon concerned was in some way ancestral to later forms that have been classified as *Homo*, even if only in its most bloated sense. However, the doubtless complex phylogenetic signal that the Ledi-Geraru and Hadar fossils are trying to convey will only become properly apparent once rigid linearity has been abandoned, and some taxonomic sense has been brought to the situation. Merely stretching the genus *Homo* ever farther into the past will get us nowhere.

Given the deep resonances involved in assigning any fossil form to the genus that we *Homo sapiens* define, it is remarkable how little objection has been raised in the anglophone literature to turning our very own genus into a taxonomic

wastebasket. One voice in the wilderness was that of Bernard Wood, once a loyal member of Richard Leakey's nominophobic team, who complained in 1992 that the genus *Homo* as then generally recognized was in all likelihood neither monophyletic nor morphologically coherent. In 1999 Wood returned to the subject in collaboration with his student Mark Collard (Wood and Collard 1999), pointing out that there were no generally agreed criteria for classifying a fossil in *Homo*. The two researchers suggested that membership in our genus should be reserved for hominins that were demonstrably more closely related to *Homo sapiens* than they were to australopiths, and that showed similarities to the living species in body mass, limb, and jaw proportions. These suggestions were hardly prescriptive in terms of detailed morphology, and they implicitly depended on the *Australopithecus/Homo* dichotomy; but they did return *Homo sapiens* to primacy as the standard by which other hominin pretenders to membership in *Homo* were to be judged. And Wood and Collard's belief was clear that no hominin should be included in *Homo* that lacked substantial stature, long legs, short arms, small jaws, reduced dentitions, relatively large braincases, delayed development schedules, and evidence of obligate bipedality. Unfortunately, Wood and Collard ultimately reverted to the Mayrian mindset in insisting on "adaptive coherence" rather than on morphology as the key unifying taxonomic criterion; but they did paint a broad picture of what a member of the genus *Homo* should look like, and it was a picture that clearly excluded *Homo habilis*, *Homo rudolfensis*, and all the supposed "*Homo* sp." fossils from the period before about 2 myr ago.

This was a welcome clean-up of the genus *Homo*, restricting the taxon as it did to *Homo ergaster*, *Homo erectus*, and later big-brained hominins, all of which share relatively large cranial volumes and the basics of modern body form, and together constitute a reasonably compact and defensibly monophyletic group. On the minus side, however, Wood and Collard had no helpful suggestions for what should be done with the forms that they excluded from *Homo*,

an omission that brings us back to the *Homo/Australopithecus* dichotomy that has for so long impeded the recognition of phylogenetic structure within Homininae. Without any broader resolution it was inevitable that the baby would eventually go out with the bathwater, and Wood and Collard's sage advice about the necessity of creating a morphologically coherent vision of our genus has subsequently been honored very much in the breach. Within a decade or two of their review, *floresiensis*, *georgicus*, *naledi* and *luzonensis* had all been unceremoniously dumped into *Homo*, along with all the hoary old favorites and some new ones too. We were back to square one (Tattersall 2014).

One final taxonomic note. It is one thing to be misguided in the subjective recognition of taxa, and entirely another to misunderstand the objective rules by which those taxa are named. But, amazingly enough, paleoanthropologists have proven to be enduringly and outstandingly good at both. In the second instance, this is because the cavalier attitude toward zoological naming to which Franz Weidenreich rather guiltily confessed is still alive and well today. An instance in point is the recent contribution, in a major journal, by Roksandic et al. (2021). These authors proposed the new species name *Homo bodoensis* for the large assemblage of European, African and Asian fossils that is generally taken to include the partial cranium recovered in 1976 from middle Pleistocene sediments at Bodo d'Ar in Ethiopia. Nowadays this entire assemblage is most commonly placed in the species *Homo heidelbergensis*, the name given long ago to a jaw discovered near the eponymous German city. Well, there is certainly a case to be made that the Bodo cranium is distinctive enough from the other *heidelbergensis* materials to be placed in its own species. But that is not the case that Roksandic and colleagues make when they reject the *heidelbergensis* name on a series of rather unusual grounds, and push instead for their new nomen. Almost incredibly, their first objection to calling the whole group *H. heidelbergensis* is that the holotype mandible was named in 1908, before the Synthesis was developed. For the very same

reason you could, of course, reject the nomen *H. sapiens* (and, for that matter, the entire contents of Linnaeus's *Systema Naturae*: Linnaeus 1758). Roksandic et al. next question the reasons why researchers in the 1980s revived the *heidelbergensis* nomen for the wider group of Middle Pleistocene fossils, without bothering to consider the crucial question of whether this view of the species actually holds up in morphological terms (as it probably does: Schwartz and Tattersall 2005) – though the Roksandic group would certainly have the right to disagree that it does, if only they were willing to cite some morphology in support of their contention.

Guided by the breathtakingly dubious proposition that “the revival of taxonomic names rarely produces desirable clarity,” Roksandic and colleagues then proceed to blithely ignore the principle of priority on which the entire edifice of modern zoological nomenclature is founded, and without which there is no objective basis for deciding which name should properly be used in referring to a given species. They also appear to regret that the holotype of *H. heidelbergensis* is not more “typical” of its species, although this would seem dangerously close to a nostalgia for the nineteenth-century typology that one might suppose they would prefer to avoid, given their ultra-contemporary attitude that “decolonizing anthropology ... should take precedence over rigid taxonomic rules.” This last, and entirely extraneous, issue arises because Roksandic and colleagues believe that the Bodo fossil on which they wish to bestow a new name belongs to the same species as the Kabwe cranium from Zambia (formerly Northern Rhodesia), which bears the prior name *H. rhodesiensis* (Woodward 1921). They thus need a way of deep-sixing the *H. rhodesiensis* name, the problem being that the beautifully preserved and more-than-adequate-as-holotype Zambian specimen is much more complete than the Ethiopian one is. But in Roksandic et al.'s brave new world, decolonizing correctness must evidently prevail at any cost; and heaven forbid that any name with even the most indirect colonial resonances should ever sully a hominin species, priority be damned.

The Extended Synthesis

The notion of punctuated equilibria was welcomed by some evolutionary biologists. But it was initially excoriated by the many more who remained under the seductive reductionist sway of the Synthesis. “Evolution by jerks” was a phrase widely cackled, and smugly smiled at, after the concept was published in 1972. Fifty years down the line, though, Eldredge and Gould's insights have been thoroughly absorbed into the wider canon of evolutionary biology as the science has expanded, the fossil record has grown, and the multiple complexities of the evolutionary process (or, rather, processes) have become apparent once more. Indeed, so much has occurred in the half-century that has elapsed since Eldredge and Gould originally wrote that a group of evolutionary theoreticians and philosophers has recently decided the time has come for a new umbrella concept, one that will both broaden and rival the Synthesis of yore. The unfortunate name chosen for this new construct, which is designed to embrace such new areas of study as genomics (and all the other “-omics”), evolutionary developmental biology (evo-devo), niche construction, systems biology, and so forth, is the “Extended Evolutionary Synthesis” (Laland et al. 2015).

This moniker has ominous overtones for the science of paleoanthropology, and not just because it reminds us that the original Synthesis had destructively steered human evolutionary studies into a systematic dead-end: a trap from which an extension of the initial source of the problem could hardly be expected to help rescue it. What is more, many of the elements that the Extended Synthesis aspires to incorporate are more productively seen as procedural tools that will potentially help us extend and broaden our evolutionary studies, rather than as concepts that will help us change our minds about the nature of evolution itself, or about the patterns that evolution produces. As a result, while paleoanthropologists certainly need to take maximum advantage of all the many recent biological advances that impact on the evolutionary sciences, they would most

advantageously seek to do so selectively, avoiding the distortions that would necessarily be imposed by yet another reductionist umbrella paradigm.

That said, the Extended Synthesis draws attention to a whole host of putative influences on evolutionary histories that any paleoanthropologist needs at least to be aware of, and some of which are of critical importance. Evo-devo, for example, brings to mind the key consideration that developmental constraints play major roles in limiting the directions that evolution can potentially take, in addition to raising such alarming possibilities as, in the words of Muller (2017), that “homologous structures can be specified by non-homologous genes, a characteristic of the genotype-phenotype relation described by developmental systems drift ... close mapping between genotype and morphological phenotype may not represent the cause but a consequence of evolution.”

The Extended Synthesis also makes much of the advent of genomics, something that has also revolutionized paleoanthropology at the near end of the timescale. Notably, the arrival of the ability to extract aDNA sequences from the bony remains of early *Homo sapiens* and recently extinct hominins has shown us that, at the very fine levels of resolution at which paleoanthropologists often need to operate, the histories even of lineages that are morphologically or genomically distinctive may be intricately intertwined. As already noted, we now know that over their time of coexistence the morphologically well differentiated hominin species *Homo sapiens* and *H. neanderthalensis* interbred on numerous occasions (e.g., Vernot and Akey 2014), and that the former has benefited, locally at least, from genomic acquisitions from the latter (Huerta-Sanchez et al. 2014). This seems to have been the case even though, in the long run, macroevolutionary outcomes were evidently unaffected: the Neanderthals clearly became extinct recognizably as themselves, while *H. sapiens* who were morphologically and behaviorally indistinguishable from their immediate predecessors went on to take over the world. Genomic evidence also suggests that more lineages of differentiated hominins were out there in the late Pleistocene

than fossil morphologies have yet betrayed (e.g., Meyer et al. 2012; Lipson et al. 2020), the clear implication being that there was more diversification and reticulation in recent hominin history than anyone had earlier expected. Much more information of great paleoanthropological significance can be expected from this source, albeit entirely independently of whether the Synthesis is successfully extended or not.

Advances in genomics have also impacted on notions of inheritance, of which several non-genetic varieties have recently been recognized in addition to the importance of gene regulation as opposed to protein coding. The most familiar of them is epigenetics, where it has been established that cells may change the activity of genes in the absence of changed DNA sequences. Often this is achieved by the methylation of cytosines (via the attachment of small molecules to the DNA building blocks) or by the modification of histones (elements of the chromosomal structure around which DNA wraps). Such changes may be transmitted across several generations at least, or they may be repeatedly stimulated over time by similar environmental effects. Quantitative models suggest that epigenetic modifications have the potential for significant long-term effects within lineages; but although they have been implicated in various genetic defects in the clinical arena, how they might relate to the macroevolutionary patterns with which paleoanthropologists need to deal is yet to be clarified.

Another aspect of non-genetic inheritance on which the architects of the Extended Synthesis have laid much emphasis, is cultural inheritance via learning; and of course, it is has always been a truism in paleoanthropology that from the beginning, and with increasing importance as time elapsed, the cultural transmission of knowledge and behaviors has constituted a crucial aspect of human evolution. Culture was, for example, a key element of process under the Synthesis (it was what broadened the human niche so much that, according to both Mayr and Dobzhansky, there could never be more than one hominid on the planet at any one time); and it is clearly set to continue as a central focus of

paleoanthropological attention. Indeed, given modern demographics, it is highly probable that in *Homo sapiens* innovation in the cultural realm will effectively be superseded by that in the biological one (Tattersall 2009). This is the case, however, irrespective of whether or not one believes that an association with the Extended Synthesis is heuristically helpful here.

And just as views on inheritance have changed, so have views on selection. The Synthesis regarded the individual as the unit of selection; but an evident difficulty is that whole individuals are incredibly complex integrated bundles, in manifold genomic and phenotypic respects. Tampering with one aspect of an organism's biology may well have undesirable effects elsewhere. Fortunately, the notion of punctuated equilibria suggested an alternative perspective: that selection might instead take place at multiple levels (Lloyd 1988, 2005) both above and below that of the individual. Those levels range from the genetic and the cellular, through the individual, to kin selection, group selection, and on up. Fitness at these different levels of selection will express itself in different ways; and it will play different roles in the maintenance of the complex and hierarchically organized systems that species represent. Indeed, it has been mooted by an advocate of the Extended Synthesis (Muller 2017) that natural selection may in fact not only exert itself in several different ways at once, but that it may actually leak between levels. At any significant magnification, such effects would, of course, complicate the construction of evolutionary narratives, although the "hierarchy theory" (Eldredge and Salthe 1984; Eldredge 1985) that attempts both to discriminate among and to integrate the genealogical (genes, demes, species, and higher taxa) and ecological (individuals, populations, and communities) hierarchies, may ease the way forward in this respect.

One aspect of evolutionary strategy on which advocates of the Extended Synthesis have laid much emphasis (e.g., Laland et al. 2015; Muller 2017), is "niche construction." This notion invokes a feedback between the impacts an organism has on its environment today, and

the conditions that environmentally mediated selection will impose on its descendants tomorrow. It is thus claimed that the processes associated with niche construction can lead on the one hand to the fixation of alleles that under other circumstances would be deleterious, and thereby eliminated, and on the other hand to the persistence of organisms in otherwise unsuitable environments (O'Brien and Shennan 2010). Well, yes; but it is evident that, to one extent or another, every organism changes its environment merely by being part of it. Subtract any organism from an ecosystem, and you have a different ecosystem. Often the difference will be relatively minor. But some species modify their surroundings quite dramatically, as mountain gorillas do when they tear up the local vegetation during displays, thereby keeping the plant community in the early stage of succession that offers the young and tender plant shoots they desire to consume. Entire communities of herbivores do the same thing on a larger scale, when they closely crop open grasslands that would turn to bushland and woodland if left to themselves. And human beings, of course, do it in spades, by negatively altering the entire surface of the planet that supports them in a process that not even Dr Pangloss could consider adaptive. So, even though human beings as usual take the process to a ridiculous extreme, there is nothing particularly extraordinary about niche construction. It certainly does not require an extension of evolutionary theory to accommodate it.

Although students of human evolution and evolutionary psychologists occasionally toy with the idea and presumed consequences of niche construction, it is hard to argue in most cases that the Extended Synthesis has yet made much general impact on paleoanthropology. But there is one major area of exception: developmental and phenotypic plasticity. The investigation of this phenomenon has been made a major component of the Extended Synthesis (Laland et al. 2015; Muller 2017), and its attraction to paleoanthropologists has been as great as its influence has been malign. It has, of course, been known for a very long time that the ways in which organisms

develop are sensitive to the environments they occupy (viz. the classic study by Clausen and Heisey 1958). Nobody disputes that the same genotype will often produce different phenotypic expressions in different places; but although under most circumstances such differences will be modest, some paleoanthropologists have seen fit to take the notion of phenotypic plasticity to a crazy extreme. They have done this by using the phenomenon as an excuse to include wildly diverse fossil morphologies within the same species rubric, blaming huge morphological differences on the development of similar genotypes under distinctive local conditions. Once again, we find paleoanthropologists showing blind fealty to Ernst Mayr, with the influence of the Extended Synthesis on their science looking in this respect very much like that of the original Synthesis in its hardened form.

An excellent example is the recent review of *Homo erectus* by Antón et al. (2016), which doughtily defends the profligate stuffing of diverse morphologies into that single species in obeisance to the shade of Ernst Mayr. Antón and colleagues are clearly aware at some level that there is no rational morphological, temporal, geographic, or systematic justification for jamming forms like the Trinil holotype, the Nariokotome Boy, and Skull 5 from Dmanisi into the same species; but since paleoanthropological tradition by now dictates that all these fossils be interpreted as belonging to the same species, they are clearly happy to take refuge in the notion of phenotypic plasticity. This enables them to note, with breathtaking understatement, that “*H. erectus* varies more than Neanderthals,” while being apparently oblivious to the fact that this judgment is much less an expression of biology than it is of ideology. One can only hope that, at some point, the science of paleoanthropology will mature sufficiently to come to grips with the difficulties involved in extracting the evidently complex phylogenetic signals that are encoded in a hominin fossil record that is already hugely diverse morphologically, and that is becoming yet more diverse by the month. Meanwhile, all one can say is that extending the Synthesis hasn't helped very much so far.

Acknowledgments

My profound thanks go to Professors Giorgio Manzi and Giovanni Destro-Bisol for so kindly inviting me to contribute these thoughts on the history of paleoanthropology to this very special issue of a very special journal. Should some readers have detected a curmudgeonly note here and there, I hasten to reassure them that I am fully aware of my enormous debt to the giants of paleoanthropology's history on whose shoulders I am standing. And I am also keenly conscious of the fact that what I have presented here is a picture taken from only one of many possible angles. Getting to my current vantage point was a tortuous process, and at the very least I feel I should record my appreciation to my extraordinary teachers, David Pilbeam and the late Elwyn Simons, who introduced me to the Synthesis, and to my friends and colleagues Niles Eldredge and the late Steve Gould for showing me, many years ago now, that there is life beyond it. Stefano Dominici kindly provided the portrait of Giambatista Brocchi and Dave Bergman the image of Lamarck; Don McGranaghan drew Figure 2 and Patricia Wynne drew Figures 3 and 4. Thank you all. And finally, a special nod must go to the memory of Ernst Mayr, without whose intervention paleoanthropology would almost certainly be a much less interesting place today.

References

- Antón S, Taboada HG, Middleton ER et al (2016) Morphological variation in *Homo erectus* and the origins of developmental plasticity. *Phil Trans R Soc B*. 371:20150236. <http://dx.doi.org/10.1098/rstb.2015.0236>.
- Berger LR, Hawks J, de Ruiter D et al (2015) *Homo naledi*, a new species of the genus *Homo* from the Dinaledi Chamber, South Africa. *eLife* 4. <https://doi.org/doi:10.7554/eLife.09560>.
- Boule M (1911-13) L'homme fossile de La Chapelle-aux-Saints. *Ann Paleont* 6 (1911):1-64; 7 (1912):65-208; 8 (1913):209-279.
- Brocchi G (1814) *Conchologia Fossile Subalpennina*, Stampa Reale, Milano.

- Brown F, Harris J, Leakey REF, Walker A (1985) Early *Homo erectus* skeleton from west Lake Turkana, Kenya. *Nature* 316:788-792. <https://doi.org/10.1038/316788a0>
- Brown P, Sutikna T, Morwood M et al (2004) A new small-bodied hominin from the Late Pleistocene of Flores, Indonesia. *Nature* 431:1055-1061. <https://doi.org/10.1038/nature02999>
- Clausen J, Heisey WM (1958) Experimental studies on the nature of species, Volume IV: Genetic structure of ecological races. Publication 165, Carnegie Institute of Washington, Washington DC.
- Darwin CR (1859) *On the Origin of Species by Natural Selection*, John Murray, London.
- Darwin CR (1871) *The Descent of Man, and Selection in Relation to Sex*, John Murray, London.
- Dembo M, Matzke NJ, Mooers AO, Collard M (2015) Bayesian analysis of a morphological supermatrix sheds light on controversial fossil hominin relationships. *Proc Roy Soc B* 282: 20150943. <https://doi.org/10.1098/rspb.2015.0943>
- Détroit F, Mijares AS, Corny J et al (2019) A new species of *Homo* from the late Pleistocene of the Philippines. *Nature* 568:181-186. <https://doi.org/10.1038/s41586-019-1067-9>
- Dirks PHGM, Roberts EM, Hilbert-Wolf H et al (2017) The age of *Homo naledi* and associated sediments in the Rising Star Cave, South Africa. *eLife* 6:e24231. <https://doi.org/doi:10.7554/eLife.24231>.
- Dobzhansky T (1937) *Genetics and the Origin of Species*, Columbia University Press, New York.
- Dobzhansky T (1944) On species and races of living and fossil man. *Am J Phys Anthropol* 2:251-265.
- Dobzhansky T (1962) *Mankind Evolving*, Yale University Press, New Haven, CT.
- Eldredge N (1979) Alternative approaches to evolutionary theory. *Bull Carnegie Mus Nat Hist* 13:17-79.
- Eldredge N (1985) *Unfinished Synthesis: Biological Hierarchies and Modern Evolutionary Thought*, Oxford University Press, Oxford.
- Eldredge N, Gould SJ (1972) Punctuated equilibria: An alternative to phyletic gradualism. In: Schopf TJM (ed) *Models in Paleobiology*, San Francisco, Freeman Cooper, p. 82-115.
- Eldredge N, Salthe SN (1984) Hierarchy and evolution. *Oxford Rev Evol Biol* 1:182-206.
- Eldredge N, Tattersall I (1975) Evolutionary models, phylogenetic reconstruction, and another look at hominid phylogeny. In: Szalay FS (ed) *Approaches to Primate Paleobiology*, S. Karger, Basel, p. 218-243.
- Fisher RA (1918) The correlation between relatives on the supposition of mendelian inheritance. *Trans R Soc Edinburgh* 59:399-433.
- Gould SJ (1983) The hardening of the modern synthesis. In: Grene M (ed) *Dimensions of Darwinism*, Cambridge University Press, Cambridge, p. 71-93.
- Groves CP, Mazak V (1975) An approach to the taxonomy of the Hominidae: Gracile Villafranchian hominids of Africa. *Casopis pro Mineralogii Geologii* 20:225-47.
- Gradstein FM, Ogg JG, Smith AG. (eds) (2004) *A Geologic Time Scale*, Cambridge University Press, Cambridge.
- Holloway RL, Broadfield DC, Yuan M (2004) *The Human Fossil Record, Vol 3: Brain Endocasts. The Paleoneurological Evidence*, Wiley-Liss, Hoboken NJ.
- Howell FC (1951) The place of Neanderthal man in human evolution. *Am J Phys Anthropol* 9:379-416.
- Howell FC (1952) Pleistocene glacial ecology and the evolution of "Classic Neanderthal" man. *Southwest J Anthropol* 8:377-410.
- Howell FC (1957) The evolutionary significance of variation and varieties of "Neanderthal" man. *Quart Rev Biol* 32:330-347.
- Huerta-Sánchez E, Jin X, Asan et al (2014) Altitude adaptation in Tibetans caused by introgression of Denisovan-like DNA. *Nature* 512:194-197. <https://doi.org/10.1038/nature13408>
- Huxley J (1942) *Evolution: The Modern Synthesis*, Allen and Unwin, London.
- Huxley TH (1863) *Evidence as to Man's Place in Nature*, Williams & Norgate, London.

- Kampourakis K (2017) Making sense of genes, Cambridge University Press, Cambridge.
- Keith A (1915) The antiquity of man, Williams and Norgate, London.
- Keith A (1931) New discoveries relating to the antiquity of man, Williams and Norgate, London.
- Laland KN, Uller T, Feldman ME et al (2015) The extended evolutionary synthesis: Its structure, assumptions and predictions. *Proc R Soc B* 282:20151019. <https://doi.org/10.1098/rspb.2015.1019>
- Lamarck J-B (1819) Philosophie zoologique, Deterville, Paris.
- Leakey LSB (1959) A new fossil skull from Olduvai. *Nature* 184:491-493.
- Leakey LSB (1961) New finds at Olduvai Gorge. *Nature* 189:649-650.
- Leakey LSB, Evernden JF, Curtis GH (1961) Age of Bed I, Olduvai Gorge, Tanganyika. *Nature* 191:478-479.
- Leakey LSB, Tobias PV, Napier JR (1964) A new species of *Homo* from Olduvai Gorge. *Nature* 202:7-9.
- Leakey M, Spoor F, Brown FH et al (2001) New hominin genus from eastern Africa shows diverse middle Pliocene lineages. *Nature* 410:433-440. <https://doi.org/10.1038/35068500>
- Leakey REF (1972) Further evidence of Lower Pleistocene hominids from East Rudolf, North Kenya. *Nature* 237:264-269.
- Lipson M, Ribot I, Mallick S et al (2020) Ancient West African foragers in the context of African population history. *Nature* 577: 665-670. <https://doi.org/10.1038/s41586-020-1929-1>
- Lloyd EA (1988) The semantic approach and its application to evolutionary theory. *PSA: Proc Biennial Meeting of the Philosophy of Science Assoc*, 2:278-285. <https://doi.org/10.1086/psaprocbienmeetp.1988.2.192890>
- Lloyd EA (2005) Units and levels of selection. In: Zalta EN (ed) *The Stanford Encyclopedia of Philosophy*. <https://plato.stanford.edu/archives/spr2020/entries/selection-units/>.
- Lordkipanidze D, Jashashvili T, Vekua A et al (2007) Postcranial evidence from early *Homo* from Dmanisi, Georgia. *Nature* 449:305-310. <https://doi.org/10.1038/nature06134>
- Lordkipanidze D, Ponce de León MS, Margvelashvili A et al (2013) A complete skull from Dmanisi, Georgia, and the evolutionary biology of early *Homo*. *Science* 342:326-331. <https://doi.org/10.1126/science.1238484>
- Mayr E (1942) Systematics and the origin of species. Columbia University Press, New York.
- Mayr E (1950) Taxonomic categories in fossil hominids. *Cold Spring Harbor Symp Quant Biol* XV:109-118.
- Meyer M, Kircher M, Gansauge MT et al (2012) A high-coverage genome sequence from an archaic Denisovan individual. *Science* 338:222-226. <https://doi.org/10.1126/science.1224344>
- Meyer M, Arsuaga JL, de Filippo C et al (2016) Nuclear DNA sequences from the Middle Pleistocene Sima de los Huesos hominins. *Nature* 531:504-507. <https://doi.org/10.1038/nature17405>.
- Morgan TH, Sturtevant AH, Muller HJ, Bridges AC (1915) *The Mechanism of Mendelian Heredity*, Henry Holt, New York.
- Muller G (2017) Why an extended evolutionary synthesis is necessary. *Interface Focus* 7:20170015. <http://dx.doi.org/10.1098/rsfs.2017.0015>.
- O'Brien M, Shennan S (2010) *Innovation in Cultural Systems*, MIT Press, Cambridge, MA.
- Olby R (1979) Mendel no mendelian? *Hist Sci* 17: 53-72. <https://doi.org/10.1177/007327537901700103>
- Reich DA, Green RE, Kircher, R et al (2010) Genetic history of an archaic hominin group from Denisova Cave in Siberia. *Nature* 468:1053-1060. <https://doi.org/10.1038/nature09710>
- Reich DA (2019) *Who we are and how we got here: Ancient DNA and the new science of the human past*, Vintage Books, New York.
- Rightmire GP, Lordkipanidze D, Vekua A (2006) Anatomical descriptions, comparative studies and evolutionary significance of the hominin skulls from Dmanisi, Republic of Georgia. *J Hum Evol* 50:115-141. <https://doi.org/10.1016/j.jhevol.2005.07.009>
- Roksandic M, Radovic P, Wu X-J, Bae CJ (2021) Resolving the “muddle in the middle”: The case

- for *Homo bodoensis*, sp. nov. *Evol Anthropol* 31:20-29. <https://doi.org/doi.org/10.1002/evan.21929>.
- Robinson JT (1953) *Meganthropus*, australopithecines, and hominids. *Am J Phys Anthropol* 11:1-38.
- Schwartz JH, Tattersall I (2005) The Human Fossil Record, vol. 4: *Australopithecus*, *Paranthropus*, *Orrorin*, and Overview, Wiley-Liss, Hoboken NJ.
- Schwartz JH, Tattersall I, Zhang C (2014) Comment on "A complete skull from Dmanisi, Georgia, and the evolutionary biology of early *Homo*." *Science* 344:360-a. <https://doi.org/10.1126/science.1238484>
- Simpson GG (1944) *Tempo and mode in evolution*, Columbia University Press, New York.
- Sturtevant AH (1913) The linear arrangement of six sex linked factors in *Drosophila*, as shown by their mode of association. *J Exp Zool* 14:43-59.
- Tattersall I, Eldredge N (1977) Fact, theory and fantasy in human paleontology. *Am Sci* 65:204-211.
- Tattersall I (1996) Paleoanthropology and pre-conception. In: Meikle WE, Howell FC and Jablonski NG (eds), *Contemporary Issues in Human Evolution*. *Cal Acad Sci Memoir* 21:47-54.
- Tattersall I (2009) *The Fossil Trail: How we know what we think we know about Human Evolution*, Oxford University Press, New York.
- Tattersall I (2014) Defining and recognizing the genus *Homo*. *Gortania* 36:5-22.
- Tattersall I (2015) *Homo ergaster* and its contemporaries. In: Henke W and Tattersall I (eds) *Handbook of paleoanthropology*, Vol 3, Springer Verlag, Heidelberg, p. 1633-1653.
- Tattersall I (2017) Species, genera, and phylogenetic structure in the human fossil record: A modest proposal. *Evol Anthropol* 26:116-118. <https://doi.org/10.1002/evan.21523>
- Vernot B, Akey JM (2014) Resurrecting surviving Neandertal lineages from modern human genomes. *Science* 343:1017-1021. <https://doi.org/10.1126/science.1245938>
- Villanea FA, Schraiber JG (2019) Multiple episodes of interbreeding between Neanderthal and modern humans. *Nat Ecol Evol* 3:39-44. <https://doi.org/10.1038/s41559-018-0735-8>
- Villmoare B, Kimbel WH, Seyoum C, Campisano CJ et al (2014) Early *Homo* at 2.8 Ma from Ledi-Geraru, Afar, Ethiopia. *Science* 347:1352-1355. <https://doi.org/10.1126/science.aaa1343>
- Washburn SL (1951) *The New Physical Anthropology*. *Trans NY Acad Sci* 13, Ser II:298-304.
- Wood BA (1999) *Homo rudolfensis* Alexeev, 1986: Fact or phantom? *J Hum Evol* 36:115-118. <https://doi.org/10.1006/jhev.1998.0246>
- Wood BA (1992) Origin and evolution of the genus *Homo*. *Nature* 355:783-790. <https://doi.org/10.1038/355783a0>
- Wood BA, Collard M (1999) The human genus. *Science* 284:65-71. <https://doi.org/10.1126/science.284.5411.6>
- Woodward AS (1921) A new cave man from Rhodesia, South Africa. *Nature* 108:371-372.
- Wright S (1932) The roles of mutation, inbreeding, crossbreeding, and selection in evolution. *Proc. 6th Int Congr Genetics* 1:356-366.



This work is distributed under the terms of a Creative Commons Attribution-NonCommercial 4.0 Unported License <http://creativecommons.org/licenses/by-nc/4.0/>

