

Special Issue: Niche Construction, Plasticity, and Inclusive Inheritance: Rethinking Human Origins with the Extended Evolutionary Synthesis, Part 1

Let Sleeping Syntheses Lie

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ABSTRACT

As the twentieth century neared its midpoint, paleoanthropology was in dire need of revitalization and some coherent concept of evolution. Sadly, as introduced to paleoanthropology by Ernst Mayr in 1950, the Modern Evolutionary Synthesis proved disastrous in this role. Far from aligning the study of human evolution with the rest of paleontology, Mayr's reductionist intervention merely alienated paleoanthropologists of all stripes from the systematics that must underpin all evolutionary biological inquiry; and it ultimately resulted in a minimalist taxonomy that did not admit adequate taxa to express systematic diversity within the rapidly expanding hominin fossil record. Since Mayr's intervention, evolutionary biology has moved on, and it is clearly necessary to incorporate important subsequent advances (punctuated equilibria, genomics, epigenetics, multilevel selection, etc.) into paleoanthropological/paleontological practice. But to do so by grafting them onto the reductionist Synthesis will simply take us farther down the blind alley in which we are already mired, while doing nothing to fix the serious systematic problem. It is also necessary to be cautious in applying key components of the proposed Extended Evolutionary Synthesis to paleontological contexts. Developmental plasticity is, for example, always a potential complication when determining species in the fossil record; but as applied to hominins it has been taken to preposterous extremes, for example, in justifying the shoehorning of a ludicrous variety of morphologies into the catch-all "species in the middle" *Homo erectus*: all in obeisance to the shade of Mayr, who likely had never seen an original hominin fossil.

PALEOANTHROPOLOGY, SYSTEMATICS, AND THE SYNTHESIS

Before embarking on the question of what the Extended Evolutionary Synthesis potentially has to offer the study of human origins, it seems relevant to note that the original collision of paleoanthropology with the Modern Evolutionary Synthesis ("the Synthesis") had equivocal results at best. The Synthesis had originally developed, over the quarter-century preceding World War II, as a rapprochement among population geneticists, developmental biologists, systematists, and paleontologists (Mayr 1982). Practitioners of all these disciplines had been wrestling independently with the implications for their particular sciences of the Darwin/Wallace theory of evolution and

the turn-of-the-century birth of particulate genetics; and gradually they found a convergence (Mayr 1982). Starting roughly with Ronald Fisher's "infinitesimal model" of 1918 and culminating with the book-length treatments of Theodosius Dobzhansky (1937), Ernst Mayr (1942), Julian Huxley (1942), and George Gaylord Simpson (1944), the Modern Synthesis integrated Darwinian ideas of natural selection with the behavior of the geneticists' alleles in natural populations. But while its more nuanced early versions had acknowledged the many exceptions that seemed to exist to almost any rule, the Synthesis rapidly "hardened" (Gould 1983) into a reductionist formula that saw evolution as a gradual, long-term process involving the accumulation of small genetic mutations and recombinations

within each population (lineage) of organisms. This slow accretion of changes occurred under the control of natural selection, as individuals with advantageous heritable features outcompeted those less favored in the reproductive stakes. Over long periods of time large effects would result from the build-up of minor changes, thereby propelling not only the slow modification of lineages but also such higher-level phenomena as the origin of new species, and even biodiversity itself.

The field of paleoanthropology came late to the Synthesis party. This was perhaps not entirely surprising, because unlike the other areas of paleontology that had been born in the early nineteenth century from geology and comparative anatomy (both of which provided wider context), paleoanthropology emerged independently during the final decades of the nineteenth century, as antiquarians and others sent ancient human bones they had found to physicians and human anatomists for analysis. There was, of course, a pretty compelling logic behind this—after all, for the first quarter-century of paleoanthropology the only ancient human bones known were either those of *Homo sapiens* or the postcranially very similar *H. neanderthalensis*, and who knew human bones better than anatomists? The problem was, though, that with their laser-like focus on the minutiae of variation within *Homo sapiens*, the anatomists neither knew nor cared very much about the broader zoological context within which their fossil bones needed to be fitted. And, while given the dimension of time within which the fossils existed they realized that a nod toward evolution was somehow appropriate, they neither knew nor cared much about the processes behind it. Perhaps the most famous early-twentieth-century English treatise on human evolution was Sir Arthur Keith's (1915) *The Antiquity of Man*, which delivered on its title to the extent that its author delved quite deeply into geological context; but you will scour the book's index in vain for any mention of natural selection. Similarly, little thought was given to the niceties of zoological nomenclature. Paleontologists in other disciplines understood that the hierarchy of taxonomic names should strive to reflect underlying phylogeny; but the paleoanthropologists basically used names at only two levels: the species and the genus. And, as it happened, the zoological binomen was conveniently analogous to the family and given names they themselves possessed. They thus casually used zoological nomina in much the same way, as identifiers for particular fossils. As the distinguished anatomist and paleoanthropologist Franz Weidenreich was quoted as saying (Mayr 1950: 109):

"it always was and still is the custom to give generic and specific names to each new type without much concern for the kind of relationship to other types formerly known."

The result was that, by the middle of the twentieth century, there were at least fifteen different generic terms in use for a relatively small handful of fossils that are all subsumed in the genus *Homo* today. And clearly, this way of

doing business was going to be untenable in the long term. What the early paleoanthropologists did share with their paleontological colleagues, however, was an authoritarian style—scholarship involved "expert judgment," wherein seniority and reputation were critically important. Subjective and usually arbitrary perception ruled the day; and, while the resulting judgments were fine so long as confidence in them persisted, they were fragile and hard to defend if questioned.

Enter the ornithologist and evolutionary theorist Ernst Mayr, one of the primary architects of the Synthesis and a leading expert on species and speciation. In 1950, Long Island's primarily biomedical Cold Spring Harbor Laboratory hosted a prestigious meeting (co-organized by the anthropologist Sherwood Washburn) on the *Origin and Evolution of Man*, that was attended by a who's who of human biologists and geneticists of the period, plus some outsiders such as Mayr and his paleontologist colleague George Gaylord Simpson. The symposium and its resulting publication were enormously influential, but without question the presentation of greatest long-term consequence was Mayr's disquisition on "Taxonomic categories in fossil hominids." That is not, of course, to suggest that the other giants of the Synthesis did not share Mayr's views—several years earlier, for example, Theodosius Dobzhansky had already expressed his belief that

"on the basis of the available data there is no reason to suppose that more than a single hominid species has existed on any time level in the Pleistocene" (Dobzhansky 1944: 265).

And the following year Simpson, for his part, had roundly criticized the taxonomic competence of those who worked on primates generally, and on hominins in particular, and had observed that

"All specimens of fossil hominids that differ in any discernible way from *Homo sapiens*, and some that do not, have at one time or another been placed in different genera. Almost none ... [of those genera] ... has any zoological reason for being. All known hominids, recent or fossil, could well be placed in *Homo*." (Simpson 1945: 188).

Nonetheless, and possibly due at least in part to wartime disruptions, such sentiments, however heartfelt and strongly expressed, had made little impact; and it was Mayr's sustained attack at Cold Spring Harbor that made a deep and lasting impression. With no pretense at ceremony, Mayr echoed Simpson in bluntly telling the physical anthropologists in the audience that, because of their "very intense occupation with only a very small fraction of the animal kingdom," their systematic standards "differ[ed] greatly from those applied in other fields of zoology." And that this had led to what he clearly considered to be a misbegotten "attempt to express every difference of morphology, even the slightest of them, by a different name" (Mayr 1950: 109).

Championing "population thinking," Mayr made it

plain that all of this was entirely deplorable, especially in having created an entirely illusory impression of great diversity in the limited hominin (at the time, hominid) fossil record then known. Instead, he declared, the opposite applied. The entire hominin fossil record contained a mere three species, all of them belonging to the genus *Homo*. What's more, the three composed a single, gradually evolving lineage. According to Mayr, *Homo transvaalensis* (what we would now call the australopiths) had insensibly given rise to *Homo erectus*, which had in turn gradually yielded to *Homo sapiens* (within which he included the Neanderthals). Any discontinuities in the known morphological record were, by implication, simply artifacts of an incomplete fossil record; and, though discretely named, the three species had no morphological or behavioral boundaries in time. Mayr even had an ecological rationale for this:

"Man," he declared, "has specialized in despecialization ... if the single species man occupies successful all the niches that are open for a *Homo*-like creature, it is obvious that he cannot speciate" (Mayr 1950: 116).

The audience was stunned, and not simply because it was hearing this gradualist and linearist dogma from a man who was already emerging as a leading scholar of speciation and, by extension, of lineage splitting. It was also because Mayr had launched his assault at a critical moment in the history of physical anthropology. As the twentieth century reached its midpoint, the prewar generation of older anatomists was ageing out, to be replaced by a cohort that, largely under the urging of Washburn (Washburn 1951), was about to inaugurate the "New Physical Anthropology" that advocated ditching old-fashioned typology in favor of flashier and more experimental studies of behavior and function. Both factions were represented in the audience at Cold Spring Harbor. The older paleoanthropologists among them were quite probably subliminally aware that they were on shaky theoretical ground; but they lacked a fallback position. In their turn, the New Physical Anthropologists were ready to reject everything that Mayr was deploring as a matter of principle. But while their reasons for abandoning long-standing tradition may have been different, both groups were primed by circumstance to capitulate to Mayr's onslaught.

There can be no doubt that Mayr had a valid complaint about the deficiencies of prevailing paleoanthropological nomenclatural practice, even though in hindsight it is obvious that he chose to take his remedy to a wildly unrealistic extreme (Tattersall 2009). But even he might have been surprised by the effects of his broadside. That is because, far from helping to push paleoanthropology into line with other areas of paleontology by encouraging more rational taxonomic standards within the profession, it caused both the Old Guard and the Young Turks to shun taxonomy and zoological nomenclature entirely. For well over a decade, anglophone paleoanthropologists had difficulty bringing themselves to use formal taxonomic names at all. Instead, they followed Mayr's recommendation (made specifically

with reference to South African australopith fossils) that

"until a real taxonomic distinction has been established ... it will be safer and more scientific to refer [to them] by vernacular names" (Mayr 1950: 113).

It is hardly surprising that the South African John Robinson (1953) soon raised his voice in print against Mayr's hominid phylogeny, pointing out that the gracile and robust australopiths were undoubtedly separate lineages—a point that Mayr (1953) rapidly, if grudgingly, conceded. Indeed, what is more remarkable is that Robinson was virtually the only paleoanthropologist to object. Across most of the anglophone world, students of the human fossil record simply shied away from zoological names entirely, preferring to follow Mayr's advice and to refer to "Steinheim," or "Qafzeh 6," or "Trinil," or whatever. Visual representations of hominin phylogeny in this period lost their tree-like branching character, and typically took the form of large billowing blobs within which those individual specimens floated in varying proximities.

Even after the use of taxonomic names had resumed in paleoanthropology once Louis Leakey and colleagues (1964) had for their own reasons blown the genus *Homo* wide open with *Homo habilis*, Mayr's legacy lingered in the form of an obstinate taxonomic minimalism that not only continued to keep the study of human fossils at a long arm's length from the study of all other vertebrate fossils, but that also balked at the creation of new species, and especially at the naming of the new genera that might have helped reflect the phylogenetic structure that was becoming increasingly obvious in a steadily expanding hominin record. Today, it is not very unusual to see a new hominin species occasionally named both early and late in the human family tree; but (except for very early forms) as far as genera are concerned, the current taxonomic algorithm seems to be a simple one: "If it's hominin and isn't *Australopithecus*, it's *Homo*." Or vice versa. This is an intellectually shoddy approach to taxonomy, to put it mildly; and, in effect, it has meant that as far as hominins of the past two million years are concerned, there is only one generic slot into which to place almost any hominin fossil, irrespective of morphology. How else is it possible to justify a genus *Homo* that includes *Homo sapiens*, the Flores form exemplified by LB1, and the Dmanisi skull D4500/2600?

The price we pay for this minimalism is high. For, while it is true that there is no theoretical upper limit to the number of species that can be shoehorned into a genus, if you squeeze in too many you are guaranteed to lose the phylogenetic signal that membership in any supraspecific taxon must encode if it is to mean anything at all. Right now, the only thing predictable about any hominin fossil classified in the genus *Homo* is that someone, somewhere, thinks it is not *Australopithecus*. Its classification in the bloated human genus effectively says nothing about its morphology, or even its phylogenetic position. As a result, however well-intentioned Ernst Mayr may have been when he tried to bring the Modern Synthesis into paleoanthropology (or

maybe it was just Ernst being Ernst), one can only conclude that, at least in the systematic realm, the results of his intervention were worse than disastrous, leaving the field almost three-quarters of a century later with no theoretical systematic backbone and in total taxonomic disarray.

Fortunately, none of this is to deny that in some broader sense the Synthesis had a positive effect on paleoanthropology. With its emphasis on natural selection and adaptation, the Synthesis opened up the study of human evolution in a new way. Prewar paleoanthropology had, quite frankly, been rather dry and procedural. Except for figures such as Raymond Dart, who could not write a dull word, Franz Weidenreich, who was prepared to go out on a limb about cannibalism at Zhoukoudian, and the cartoonists who never tired of caricaturing the Neanderthals, the prewar paleoanthropological literature had tended to lack the sense of life that any satisfying account of human evolution needs to have at its core. In contrast, and particularly beginning in the early 1950s with Clark Howell's work on the Neanderthals (Howell 1951, 1952), the entire aspect of the anglophone paleoanthropological literature changed, as its authors integrated aspects of adaptation, ecology, morphology, time, and behavior into their evolutionary scenarios. As time passed, the development of paleoanthropology as an explanatory as opposed to purely descriptive science began to owe more and more to advancing technology; but it is undeniable that the beginnings of this entirely commendable trend were underwritten by the spirit of the Synthesis.

POST-SYNTHESIS DEVELOPMENTS

Most commonly in its hardened versions, the Synthesis continued to dominate evolutionary biology including paleoanthropology until the early 1970s, when the paleontologists Niles Eldredge and Stephen J. Gould (1972) offered the alternative to its "phyletic gradualism" that they termed "punctuated equilibria." The Synthesis had given rather short shrift to paleontology, regarding its fundamental unit of analysis, the species, as merely ephemeral. For, while species might be spatially and reproductively bounded at specific moments in time, the Synthesis saw them as gradually evolving themselves out of existence over the eons. Eldredge and Gould undiplomatically pointed out that, in stark contrast, the message of the actual fossil record appeared to be otherwise. Species, like individuals, have births, lifetimes, and deaths. They tend to appear abruptly in the stratigraphic record, to linger for varying but sometimes very extended periods, and then to disappear to be replaced, often but not invariably by a close relative. Stasis abounds; and significant change, Eldredge and Gould argued, tends to happen in short-term speciation events that occur on the periphery of species' ranges and are unlikely to be captured in the fossil record. Reproductive competition among individuals was evidently not the principal driver of evolutionary change. Instead, external events entirely adventitious to the biological structure of any given group of organisms appeared to have the greatest influence on shaping larger evolutionary patterns. Such events might

include climatic and environmental change, the advent of other species, and entire faunal turnovers; and all at some level emphasized the importance in evolution of interspecies competition. This realization rapidly gave rise to notions of multilevel selection and then to hierarchy theory (Vrba and Eldredge 1984).

Additionally, it emerged that there are good reasons to doubt that the principal function of natural selection, at least in the classic Darwinian sense, is as the agent of change envisaged by the Synthesis (Tattersall 2012). After all, selection (which is admittedly a mathematical certainty in any species in which more individuals are born than survive to reproduce) acts not on individual traits, but on individual organisms. And whole, functioning organisms are incredibly complex and integrated packages that are governed at the genetic and developmental levels by astonishingly intricate mechanisms of pleiotropy and polygenicity. No change comes without penalty; and as a result, in most cases the main function of natural selection seems to be to trim the unviable extremes from both ends of any distribution of interest, rather than to promote one of those extremes. Natural selection thus emerges principally as a stabilizing influence, serving to maintain the viability of species as wholes and thereby underpinning the frequent phenomenon of extended stasis in fossil species to which Eldredge and Gould had drawn attention.

The shift in perspective occasioned by the advent of punctuated equilibria not only changed the entire macroevolutionary picture, but also re-established species as "real" units in time as well as in space, and as objective units of analysis for paleontologists. Most importantly in practical terms, it made it easier for paleontologists to adopt the more testable approach to generating phylogenies that was being urged by the then-nascent cladistics movement (Eldredge and Cracraft 1980). And ultimately, it was what made it possible to implement the quantitative tree-building approaches that dominate paleontological systematics today. In addition, of course, the new ability to build more robust phylogenies in turn brought with it the opportunity to construct more firmly based evolutionary scenarios that incorporated a flood of new information from new sources. This widening of the paleontological database was made possible by the advent of a whole panoply of chronometric dating methods, and of new ways of reconstructing ancient environments, diets, ecosystems, and so forth (see recent review by Higham 2021).

Still, while all the developments just briefly recounted have been eagerly embraced in other areas of paleontology to help produce integrated pictures of the past, paleoanthropologists have remained conflicted. They have eagerly grasped the new technologies involving visualization, environmental reconstruction, ancient diets, and so forth; but at the essential systematic level they have remained hamstrung by neo-Mayrian minimalism. Because of their reluctance to acknowledge the evident diversity that exists in the human fossil record, paleoanthropologists have naturally gravitated toward a simplistic picture of human evolution that denies the evidently highly opportunistic and

experimental nature of the hominin subfamily in general. The tendency has been instead to track the “evolution” of systems (the brain, gut, locomotion, etc.), rather than of the taxa into which they are bundled, and that are the actual targets of evolution (in the long run, it does not matter a whole lot how magnificently adapted you might be in any given feature, if your entire species is being outcompeted into extinction). The advocates of an Extended Synthesis in paleoanthropology are undoubtedly right to conclude that things need to move forward from here; but change will surely be more constructively achieved by adding an appreciation of the importance of systematics to the current paleoanthropological repertoire, than by enhancing the misguided purities of the past.

Well, “punk eek” celebrated its own half-centennial last year; and although it was doughtily resisted at the time of its proposal, and remains robustly debated, its essence survives in a more comprehensive and nuanced understanding of the complexities attending the many processes that help shape evolutionary histories. This new outlook stands in complete contrast to the reductionist simplicities of the Modern Evolutionary Synthesis, at least as Mayr foisted it upon paleoanthropology. And indeed, in the light of everything we have learned, the Synthesis in its purist form appears as a blind alley leading off the main historical track of developments in evolutionary thought. It was undoubtedly a useful heuristic in its time; and it was even perhaps an essential one, without which we could not have got to where we are. But however seductive the “change = time + selection/adaptation” equation that lies at the heart of the hardened Synthesis may be, it fails to give appropriate attention to the branching of lineages, or to capture the many nuances of evolutionary process. And it thereby distracts our attention from an evidently complex and multifactorial dynamic in which evolutionary change is largely contingent, and in which different mechanisms may be in operation in different cases. It follows, then, that unless we are careful, simply “extending” the Synthesis would just move us farther down the reductionist blind alley. And, as it has turned out, evolutionary theory has already taken another turn, or many of them, leading to a vibrant and even combative field in which no generally agreed reductionist paradigm is in sight. Indeed, it is possible to argue that no overarching paradigm appears compellingly necessary at a time when we can recognize that evolution is essentially an observed result rather than a unitary mechanism, however intricate. At this point, attempting to build on the Synthesis, rather than upon a realization that things are more complicated than the hardened Synthesis was willing to admit, simply adds an extra hurdle for evolutionary biologists to stumble over.

EXTENDING THE SYNTHESIS IN PALEOANTHROPOLOGY

Whereas the originators of punctuated equilibria were working paleontologists who were motivated by the need to explain the macroevolutionary patterns they observed in the fossil record, the early proponents of the Extended Syn-

thesis were evolutionary theoreticians and philosophers, unburdened by the immediate need to align theory with pressing empirical necessity. They saw that evolutionary biology had come a very long way since the heyday of the Modern Synthesis in the mid-twentieth century, and they logically enough concluded that, having been conceived before the advent of genomics, epigenetics, evo-devo, niche construction, developmental bias, and so forth, the Synthesis absolutely required some tweaking to accommodate such phenomena (see Pigliucci and Müller 2010, Laland et al. 2015). This remains a perfectly fair and useful perception, and not solely from the theorists’ more abstract perspective. Pigliucci and Müller (2010) and other contributors to their edited volume make a compelling case for the utility of an umbrella concept that integrates the useful attributes of the Synthesis, as developed between 1918 and the early 1940s (basically, its integration of Mendelian and populational statistical genetics with concepts of evolutionary change) with distinctive and more recent developments ranging all the way from Mayr’s formulation of the biological species notion in 1942, through punctuated equilibria in the 1970s, to epigenetics and genomics today. The active debate that the formulation of that umbrella concept has elicited has been a welcome one, although some of it has been conducted on a rather abstruse front that, for example, sees the Extended Synthesis as “a vast network of models and interweaved representations that, instantiated in diverse practices, are connected and related in multiple ways” (Fabregas-Tejada and Vergara-Silva 2018: 169). More practically, Kissel and Fuentes (2019) perceived in the Extended Synthesis an opportunity to recognize the diversity of processes that might potentially influence evolutionary histories and, when considering human evolution, to think about them in a “holistic and integrative” way. This is all well and good, but unfortunately it does little to change the reality that, for working paleoanthropologists scarred by the hardened Synthesis, the lesson of history is above all a cautionary one. Because, far from bringing their practices into line with other areas of paleontology, the paleoanthropologists’ capitulation to the Synthesis as presented by Mayr deflected the study of the human fossil record into an exceptionalist dead-end from which it has still to extricate itself. And clearly, simply extending the problem (the Synthesis) is not going to help.

This is not, of course, to suggest that paleoanthropology does not need to come to terms with the new developments in evolutionary biology that the Extended Synthesis is intended to accommodate. But it would most wisely do so incrementally, rather than in the context of some grand new paradigm. And it could also do it selectively. For example, some behavioral evolutionists find useful explanatory power in the idea of “niche construction,” whereby the activities of organisms alter their environments and therefore the selection pressures operating on them and on those organisms with which they are sympatric. It has been argued that niche construction is significant because it may lead to the fixation of otherwise deleterious alleles that would otherwise be eliminated (O’Brien and Shennan 2010). How-

ever, another way of looking at niche construction is simply as evolutionary biology's answer to the Heisenberg Uncertainty Principle. All organisms, no matter how simple, alter their own environments in some way, simply by being part of them. Not every organism affects its surroundings as dramatically as, say, the displays of mountain gorillas do when they tear up vegetation and thereby keep the local plant community in an early stage of ecological succession; or as humans do, with their nasty habits of deforestation, overfishing, and strip mining. But organisms of all kinds, and particularly entire communities of them (think grazers on the savanna or the taiga), can have significant large-scale ecological effects without changing the basic rules of the game. There is no doubt that certain phenomena can be usefully investigated from the perspective of niche construction and the dynamic view of the niche that it entails; but the concept remains as much a heuristic as an individuated phenomenon, and hardly qualifies as an extension of the basic evolutionary paradigm as currently understood.

A component of the Extended Synthesis that has been particularly attractive to paleoanthropologists is developmental plasticity, a phenomenon of which the importance was clearly understood from the very early days of genetics, long before the original Modern Synthesis was conceived. It is easy to understand this attraction because, as already pointed out, although there is a great deal of morphological variety out there in the hominin fossil record, there is a very limited number of species conventionally available to allocate it to. Accordingly developmental plasticity, the notion that the same genome will produce different morphological outcomes in different circumstances, is a god-send to anyone trying to rationalize why they are following Ernst Mayr's (1950) theoretical exhortations and squeezing endless morphologies into the same species pigeonhole. A classic case in point is Antón et al.'s (2016) review of variation in *Homo erectus*, the species, as you will recall, into which Mayr instructed that all non-australopith, non-Neanderthal/*sapiens* hominins should be placed. Antón and her colleagues accurately perceive that morphological variation within the broad Mayrian concept of that species is inordinately large, and they seek to explain it by the high developmental plasticity of a genome responding over multiple environments. The resulting and extraordinarily voluminous "*Homo erectus*" assemblage encodes a huge amount of phylogenetic history, embraces two million years of time (the entire span of any coherent concept of *Homo*: Tattersall 2014), and geographically includes all of Eurasia and Africa.

Any mammalian systematist coming fresh to this medley would find it necessary to split it into several taxa. But, still hobbled by the legacy of Mayr, many paleoanthropologists find it impossible even to contemplate this rational move; and developmental plasticity offers a welcome rationale for brushing all that inconvenient morphology under the rug, where it can be safely ignored. This is all very understandable because, as already noted, we are dealing here with a very recently evolved and closely related group, one within which morphological signals are not always going

to be very clear: homoplasy is, after all, most widespread among close relatives with similar genomes. Antón and her colleagues (2016: 1) note, entirely correctly, that "*H. erectus* varies more than Neandertals" but are reluctant to recognize that this is because their concept of *H. erectus* as the "hominin in the middle" means that it must perforce include any hominin morphologies of appropriate age that a paleoanthropologist might be prepared to stuff into it. As a result, they are obliged to accept the variational anomaly, and to take refuge in the non-taxonomic special explanation that developmental plasticity appears to provide.

Sadly, though, the reality remains that if we are ever to make progress we must grasp the morphological nettle, however uncomfortable it makes us. It has served us well in classifying the extant fauna, and it seems entirely reasonable to apply morphological standards derived from more fully documented living relatives to the classification of fossil forms. And we need to recognize that, ultimately, the developmental plasticity argument is a counsel of phylogenetic despair. For, while morphology is the only aspect of any fossil that is definitely associated with its identity (Eldredge and Tattersall 1975), if extinct hominins really did exhibit the degree of developmental plasticity that Antón et al. appear willing to accept, we can basically forget about recovering any meaningful phylogenetic signals from the morphologies preserved in the finer divisions of the human fossil record. This would be no minor loss, for without an accurate phylogenetic framework there is no way to understand the very complex history of innovations and relationships within our subfamily. So, while that does not mean that we can ignore developmental plasticity altogether, and indeed emphasizes that we need always to be aware of its implications, we should clearly remain judicious when applying the concept, and be wary of dismissing morphology out of hand.

It is perhaps also worth noting that many of the human behaviors that have been studied from the point of view of the Extended Synthesis are derived from observation of modern *Homo sapiens*, and then extrapolated back into the past well beyond the short tenure of our species. The result is that we frequently see extinct hominins as less sophisticated versions of ourselves, rather than as distinctive cognitive entities that need to be understood on their own terms. The temptation to proceed in this way is obvious. But we should nonetheless be very wary of using *Homo sapiens* as a behavioral model or even analogue for any extinct hominin because the modern human cognitive algorithm has undergone a radical restructuring in rather recent times (see Tattersall, 2012). This is not, of course, to deny that hominins have been savvy creatures from the start, and that by the late Pleistocene several hominin lineages were displaying very high intelligence, each in its own way. The best-documented extinct case of this kind is, of course, *Homo neanderthalensis*, which is nowadays regularly being documented to have done things that at one time were believed to be unique to *Homo sapiens* (see review by Wragg 2020). Evidently, you can be very smart indeed without being *Homo sapiens*.

Nonetheless, while it is evident that a large brain functioning on the ancestral, intuitive (and nondeclarative, although see Planer and Sterelny 2021 for an alternative view on the antiquity of language) algorithm can produce very impressive cognitive results, only *Homo sapiens* seems ever to have operated on the symbolic cognitive algorithm we use today (Tattersall 2017). The practical difference is that, while other organisms basically live in the world that Nature presents to them, members of modern *Homo sapiens* live for much of the time in the worlds they reconstitute in their heads. This is possible because they deconstruct their surroundings and interior experiences into a vocabulary of discrete mental symbols. They can then mentally combine and recombine those symbols, according to rules, not only to consciously describe the world as it is, but to generate new visions of it as it *might* be. This radically new way of processing information was probably stimulated in the “language-ready” (Boeckx and Benitez-Burraco 2014) *Homo sapiens* brain by the spontaneous invention of language (Tattersall 1998, 2017), at a point subsequent to the origin of our species as a distinctive anatomical entity.

The resulting shift to symbolic reasoning changed the rules by which members of our species interacted both with their conspecifics and with the exterior world. For the first time in the history of life, beginning around 100,000 years ago, Earth harbored a species both able to step back and view itself as an actor on the ecological stage, and to imagine that things could be otherwise than they are. Combined with pre-existing high manual skills, this new ability to envisage and implement change in the external environment very soon proved to be an entirely unprecedented influence on the planet, and in the event a severely damaging one. Indeed, one might fairly describe the outcome as “niche destruction.” That in evolutionary terms the underwriting switch in information processing mode was virtually instantaneous, underlines the radical and qualitative nature of the cognitive change involved. And it strongly suggests that we should be very cautious when we interpret the activities and motivations of extinct hominins in the light of what we can observe today, even when those activities were/are clearly directed to similar ends.

CONCLUSION

Following Ernst Mayr’s onslaught in 1950, paleoanthropology swiftly capitulated to a “hardened” version of the Modern Evolutionary Synthesis that preached that human evolution had consisted of the gradual modification, through time, of a single lineage. So traumatic was Mayr’s intervention that, even as the human fossil record has hugely enlarged and furnished us with ample evidence of past hominin diversity, paleoanthropologists have maintained a steadfastly minimalist attitude to hominin systematics, cramming an increasing range of morphologies into the smallest possible number of taxonomic pigeonholes. At the same time, as new areas of biology ranging from genomics to evo-devo and to epigenetics have emerged, evolutionary biologists of all stripes have been realizing the inadequacy of the Synthesis, particularly in its hardened form,

as a conceptual umbrella for, or description of, the evolutionary process. That leaves us with a stark choice—either the Synthesis has to go, or it needs to be updated with the new biology as an Extended Evolutionary Synthesis. Both the conceptual inadequacies of the Synthesis itself, and the practical experience of paleoanthropology, suggest that it would be best for students of human evolution, at the very least, to go back to the drawing board.

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STATEMENT ON USE OF AI

No AI was used in the preparation of this paper.

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