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The species in paleoanthropology

Ian TATTERSALL



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The species in paleoanthropology

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ABSTRACT

The species is the basic unit of analysis in systematic paleontology. Yet, for most of its history the subfield of paleoanthropology has lacked any coherent concept of what fossil species are, using the species epithet variously at different times – most recently, with the conspicuous effect of minimizing apparent diversity among the hominins. The application of molecular systematic techniques to the analysis of high-latitude early *Homo sapiens* Linnaeus, 1758 and its contemporaries thus offers a welcome opportunity to reappraise our approaches to species recognition in the rapidly expanding hominin fossil record. But it must be cautioned that evidence for hybridization among documented or hypothesized lineages cannot necessarily be taken as evidence for recombination among them, and that “braided stream” models of hominin evolution (which militate against speciation) cannot account for the diversity of historically and morphologically differentiated entities we see in that record.

KEY WORDS

Species,
paleoanthropology,
evolution,
hominins,
molecular systematics,
speciation,
braided evolution.

RÉSUMÉ

L'espèce dans la paléanthropologie.

L'espèce est l'unité d'analyse de base en paléontologie systématique. Mais, pendant la plus grande partie de son histoire, le sous-domaine de la paléanthropologie a manqué de tout concept cohérent de ce que sont les espèces fossiles. Les noms zoologiques ont été utilisés de diverses manières à différentes époques, bien que dernièrement avec une tendance à minimiser la diversité au sein des hominins. L'application des techniques moléculaires à l'analyse des premiers *Homo sapiens* Linnaeus, 1758 des hautes latitudes, et de leurs contemporains, offre une bonne occasion de réévaluer nos approches de la reconnaissance des espèces dans le registre fossile des hominins. Mais il faut admettre que les preuves de l'hybridation entre les diverses lignées ne peuvent pas nécessairement être considérées comme des preuves de la coalescence entre elles, et que les modèles de « flux tressés » (qui militent contre la spéciation) ne peuvent pas rendre compte de la diversité des entités historiquement différenciées que nous voyons parmi les hominins.

MOTS CLÉS

Espèce,
paléanthropologie,
évolution,
hominins,
systématique moléculaire,
spéciation,
évolution tressée.

INTRODUCTION

As the diverse contributions to this memorial symposium amply attest, Yves Coppens' long life in paleoanthropology saw vast improvements both in the archaeological and vertebrate fossil records, and in the methods employed to analyze them. Equally importantly, it also witnessed far-reaching changes not only in our theoretical concepts of evolutionary process, but in the day-to-day practice of paleontological systematics. Future historians may well conclude that some of the most significant of those latter changes began during the final quarter-century of Yves's career, when the introduction of genomic methodologies into paleoanthropology began to make it evident that sooner or later we would have to confront, head-on, the intractable question of what we are actually talking about when we refer to fossil hominin species. Of course, from the very beginnings of paleoanthropology in the mid-nineteenth century it had been taken for granted that species, and the genera into which they are grouped, are in some vague way the basic units of analysis in the hominin fossil record; but during paleoanthropology's first century or so, paleoanthropologists nonetheless typically paid little attention to the practical and theoretical implications of the zoological naming process (see e.g. Tattersall 2000; Zeitoun 2019). That was worse than unfortunate, because the ultimate aim of zoological nomenclature ultimately has to be not only to provide identifiers, but also to aid in characterizing the phylogenetic structure that exists within any diverse taxon: a structure that needs to be made explicit before any reliable further studies can be embarked upon.

NOTIONS OF THE SPECIES AND GENUS IN PALEOANTHROPOLOGY

The general insouciance relative to zoological names was still prevalent during the late 1950s, when Yves Coppens began his studies of evolutionary biology under the tutelage of Camille Arambourg. That was a time when the tradition of authoritative pronouncement by experts was still alive and well in paleontology in general; and it was particularly pervasive in the subfield of paleoanthropology. Largely, this was because the origins of hominin paleontology lay not in geology or comparative anatomy, but in the study of human anatomy – a field of inquiry that was inherently unconcerned with questions of diversity and hierarchy in nature. The influential ornithologist and evolutionary theorist Ernst Mayr neatly captured the resulting insularity in 1950 by quoting Franz Weidenreich, the eminent human anatomist and monographer of the Peking man fossils, on the matter of traditional alpha taxonomic practice in paleoanthropology. According to Mayr, Weidenreich had recalled that “It always was, and still is, the custom [in paleoanthropology] to give generic and specific names to each new type without much concern for the kind of relationship to other types formerly known” (Mayr 1950: 109). This statement was especially revealing because Weidenreich, who died in 1948, had joined Mayr at

New York City's American Museum of Natural History back in 1941, just as the latter was poised to publish his *Systematics and the Origin of Species* (Mayr 1942). That book was one of the key works of the emerging New Evolutionary Synthesis (“the Synthesis”), basically a comprehensive reformulation of evolutionary theory that reconciled Darwinian selection with a population-oriented view of genetics, and that ultimately reduced evolutionary change to little more than gradual shifts in gene frequencies under the guiding hand of natural selection.

Weidenreich himself was keenly aware of the new ideas that were roiling evolutionary biology toward the end of his career, even as he disarmingly admitted to a younger colleague that it was too late for him to change his own set ways of going about things (see anecdote cited in Tattersall 2009). His recollection thus accurately reflected the prevailing system of expert judgement just referred to, whereby a recognized authority's conclusions as to the significance of a given fossil were typically supported by little more than the eloquence and professional reputation of the individual concerned. For paleoanthropological systematics the result of this was that generic and specific names were typically flung around with a fine abandon, as experts bestowed genus and species names on their fossils pretty much as they conferred family and given names on their children. And indeed, it was squarely in this tradition that Yves Coppens himself proceeded when he described his first fossil hominins. In 1965, he named a persistently inscrutable cranium from Chad *Tchadanthropus uxoris* (Coppens, 1965); and three years later, in collaboration with his mentor, he baptized an almost equally enigmatic edentulous Ethiopian mandible *Paraaustralopithecus aethiopicus* (Arambourg & Coppens, 1968).

Long before this point, however, the intellectual developments to which Weidenreich had found it so difficult to adjust had begun to permeate mainstream evolutionary biology. In 1937, the geneticist Theodosius Dobzhansky had published his book *Genetics and the Origin of Species* (Dobzhansky 1937), the most important single foundational document of the Synthesis, and in 1944 he applied the movement's principles to human evolution. Starting from the proposition that what defines species is reproductive isolation (this was before the days of fancy acronyms for species concepts), Dobzhansky arrived at the conclusion that “no more than a single hominid species has existed on any time level in the Pleistocene” (Dobzhansky 1944: 265). Given that the relatively limited human fossil record then available was already hugely cluttered with generic names and the illusion of diversity they conferred, this was an extraordinarily radical proposal, and one that had extensive nomenclatural implications. Nonetheless, and most likely because of wartime distractions, Dobzhansky's assertion failed at the time to cause much of a stir – which is probably why, after his provocative initial intervention, the geneticist let the matter rest for almost two decades.

But the fireworks were not over, because Ernst Mayr had meanwhile brought systematics into the fold of the Synthesis with the publication of his 1942 book. And Mayr, who was ironically destined to become the leading champion of the allopatric speciation theory, soon also spotted the opening in

paleoanthropology, even though quite likely he had never seen an original hominin fossil. Accordingly, in what must have been one of the most arrogant and influential symposium presentations ever, he took aim in 1950 at what he called the “simply bewildering” diversity of genus and species names that had by then accumulated in paleoanthropology. Mayr began his diatribe by declaring that:

“The nomenclatural difficulties of the anthropologists are chiefly due to two facts. The first one is a very intense occupation with only a small fraction of the animal kingdom, which has resulted in the development of standards that differ greatly from those applied in other areas of zoology. And, secondly, the attempt to express every difference in morphology, even the slightest one, by a different name” (Mayr 1950: 109).

This was spot on. But then the ornithologist more dubiously played the theory card, upping the ante on Dobzhansky by asserting that, even in principle, the hominid ecological niche was so broad as to obviate speciation. He observed that:

“Man occupies more ecological niches than any known animal. If the single species man occupies all the niches that are open for a *Homo*-like creature, it is obvious that he cannot speciate” (Mayr 1950: 116).

And finally, after a lot more in this vein, he threw out the thicket of genus and species names that suggested high diversity among extinct hominins, and replaced it with the simple linear proposition:

Homo transvaalensis → *Homo erectus* → *Homo sapiens*

In other words, all known hominins belonged to a single three-species succession that was entirely embraced by a single genus. *Homo transvaalensis* (Broom, 1936) (what we would nowadays call the australopiths) had gradually given rise to *Homo erectus* (Dubois, 1893), which had in turn insensibly transformed into *Homo sapiens* Linnaeus, 1758 (including the Neanderthals). What was more, while his unbranching and gradually transforming hominin lineage might have been somehow objectively bounded in space, any delimitations within it were necessarily purely arbitrary, for its species lost their identities in time. And the crowning irony, given his disdain for Franz Weidenreich’s taxonomic methods, was that Mayr’s arrangement closely mirrored the “Archanthropinae → Paleoanthropinae → Neoanthropinae” sequence that Weidenreich had proposed three years earlier in one of his last published papers (Weidenreich 1947).

Probably because they had been dimly aware all along that they had been treading on thin theoretical ice, almost the entire old guard of anglophone paleoanthropology capitulated forthwith to Mayr’s linearist dogma, even though it deprived them in principle of their basic unit of analysis, the morphospecies – a notion that was, in another delicious irony, anathema to Mayr, who had brought them on side

(e.g. Mayr 1963a). The only major dissent came from the South African paleoanthropologist John Robinson (1953), who objected that diversity did indeed exist among the australopiths – a point that Mayr (1953) rapidly conceded. For their part, the younger members of the profession responded by gravitating toward the recently launched “New Physical Anthropology”, an approach to human biology that valued dynamic functional studies much more highly than it did the dusty old-time systematics of their elders. And while this was all very well as far as it went, it also meant that many of the new generation adopted the corrosive attitude that any insistence on the importance of accurate species recognition in the hominin fossil record was merely to “quibble about names” – an attitude that proved remarkably tenacious, even as it necessarily involved forgetting that sorting out the phylogenetic organization of nature is the fundamental issue that must be resolved before any other biological concerns can be broached.

Whichever the response, the effect was the same. And it was presumably not the effect that Mayr had intended for his attempt to bring paleoanthropological nomenclature into line with what he saw as more general standards in zoology. Because, paradoxically, anglophone paleoanthropologists of all stripes responded to the ornithologist’s attack by simply shying away from zoological nomenclature altogether. Zoological names were spurned in favor of references to individual fossils, and for over a decade nobody dared to publish an old-style family tree showing relationships among diverse hominin species. Something similar also occurred in francophone paleoanthropology, as many authors eventually began avoiding zoological names in favor of an informal Weidenreichian sequence running from “Archanthropiens”, “though Paléanthropiens”, to “Néanthropiens” (e.g. Genet-Varcin 1969; Saban 1972). Eventually Mayr’s linear view of the evolutionary process was also enthusiastically adopted in various guises, particularly after Loring Brace (1962, 1964) had begun arguing for temporal continuity between Neanderthals and modern humans on his way to producing a full-fledged statement of his “Single Species Hypothesis” (Brace & Montagu 1965). Brace and his co-author Ashley Montagu essentially restated the radical Dobzhansky/Mayr view of the human niche, thereby indirectly inspiring the Multiregional Evolution industry that was to emerge two decades later (e.g. Smith & Spencer 1984) – and whose proponents, in a continuing exquisite irony, came to trace its origins back to Weidenreich (Wolpoff & Caspari 1996).

As the human fossil record continued to grow, some paleoanthropologists became at least subliminally aware of the need to re-examine it for potential systematic structure. Accordingly, in the summer of 1962 an influential international meeting on “Classification and Human Evolution” was hosted by the Wenner-Gren Foundation at its Burg Wartenstein conference center in Austria. The distinguished participants, including Ernst Mayr (1963b), came from a wide variety of backgrounds (see Washburn 1963), but they fairly unanimously converged on the by then well-established minimalist approach. As reported by Campbell (1963) the group as a whole stuck with

Mayr's basic linear proposition, albeit allowing an offshoot for the "robust" australopiths and re-establishing the genus *Australopithecus* Dart, 1925 for the first stage of the sequence. The genus *Homo* Linnaeus, 1758 retained the two species *H. erectus* and *H. sapiens*, and around 100 named species were invalidated by consensus.

Still, at least one of those in attendance at Burg Wartenstein was clearly not on board with this minimalism. For two years later Louis Leakey, along with his colleagues Phillip Tobias and John Napier (also an attendee), provided a watershed moment in hominin systematics with the publication of *Homo habilis* Leakey, Tobias & Napier, 1964 from Tanzania's Olduvai Gorge (Leakey *et al.* 1964). Small-brained and dentally rather gracile-*Australopithecus*-like, this new species failed to conform to any rational idea of what a species belonging to the genus typified by *Homo sapiens* should look like. But Leakey had a famously cavalier attitude to naming new species and genera at the best of times; and as an adherent of the "Man the Toolmaker" notion he found his new hominin the best available candidate for manufacturer of the stone tools found at the bottom of the Gorge. In any event, whatever the (very dubious) merits of the new species as a member of *Homo*, from this point on both the accelerating rate of fossil hominid discovery, and the associated pressure of accumulating novel morphologies, began to force what eventually became a very substantial increase in the number of zoological names generally applied to fossil hominins. By the middle 1990s about a dozen different species were routinely recognized as hominin, and two decades later that number had approximately doubled.

It is possible that this proliferation of species was solely due to the practical need to find new pigeonholes for new morphologies. But at least in a minor way it may also have been helped along by a perceived need to rethink how hominin species should in principle be recognized in the fossil record. This perception had emerged in the wake of Niles Eldredge and Stephen Jay Gould's (1972) famous attack on the gradualist theoretical underpinnings of the Synthesis, which by then had reigned supreme for decades. Eldredge and Gould pointed out that paleontologists had long been well aware that the fossil record was riddled with "gaps" (missing transitional forms) that undermined the transformationist way of thinking about evolution. And they insisted that those gaps were real. They noted that species typically appeared abruptly in the fossil record, lingered for varying periods of time while showing little if any perceptible change, and just as abruptly disappeared. In other words, as Michael Ghiselin (1974) was about to propose, species were individuals, with births at speciation, lifespans, and deaths at extinction. Far from being arbitrarily-designated ephemera, segments of lineages that evolved themselves out of existence, species were bounded and definable entities. Eldredge and I (Eldredge & Tattersall 1975) subsequently applied this perspective to the human fossil record, concluding that it conformed much better to the new "punctuated equilibria" model than to Mayr's gradualist one. At the same time, we offered the earliest cladogram of the hominins. Originating

in the work of the entomologist Willi Hennig (1966), the cladistic approach represented a quantum leap in systematics by producing explicitly testable hypotheses of relationships among organisms, and its spirit subsequently underpinned all later advances in determining the relationships among living and extinct organisms. Because this point is so frequently misunderstood, it should be noted here that cladistics was never intended as a tool for recognizing species. It is, instead, an approach to determining relationships by descent among species previously established by other means. But it does make the importance of accurate species recognition glaringly obvious, if only because any subsequent analysis will so clearly be incorrect if not based on properly delineated units.

Our initial hominin cladogram was pretty crude, but contrary to Mayr's predictions it strongly suggested that "*Homo erectus* [...] does not present a good ancestral morphotype for *Homo sapiens*" (Eldredge & Tattersall 1975: 237). And constructing the cladogram also forced us to conclude that "we do not know how many taxa we are dealing with in our discussions of the fossil hominid material" (p. 241). This latter reflection ultimately led me to pose the question of exactly how species should be recognized in the hominin fossil record (Tattersall 1986), an exercise that immediately exposed severe procedural difficulties. For, as Eldredge and I had already observed, morphology is the only property of a fossil (the others being time and geography) that has a necessary relationship to its systematic position; and while a species may develop considerable internal morphological variety in the absence of speciation, it is equally true that speciation may take place without many observable morphological consequences, if any at all. Many colleagues responded thoughtfully to these complexities, the results ultimately including Colin Groves's *A Theory of Human and Primate Evolution* (1989) and Bill Kimbel and Lawrence Martin's edited volume *Species, Species Concepts, and Primate Evolution* (1993), in which the still-widening array of available species concepts (Coyne & Orr [2004] subsequently listed at least 25) was explicitly discussed in the context of numerous living and extinct primate groups.

Still, even a cursory examination of the literature underpinning the proliferation of lower-level hominin taxa over the last quarter of the twentieth century suggests that, despite this new awareness, most of the new names had little to do with any rethinking about what species themselves were, or about what naming them implied about evolutionary histories. Instead, fossil species continued to be widely thought of among paleoanthropologists as a kind of necessary evil needed to cope with the volume of new material, rather than as meaningful biological units that had played specific roles in nature. Of course, just by itself the burgeoning of those fossil hominin species had opened up a new and utterly un-Mayrian perspective upon the human evolutionary past, notably by making it clearly evident that multiple hominins had typically existed at any one point in time, and that far from being a story of continuous lineage improvement human evolution had involved the active generation of diversity and vigorous evolutionary experimentation. This radical change of perspective has had enormous ramifications, making it clear, for example, that the

current lonely status of modern *Homo sapiens* as the world's only representative of its group is a highly abnormal state of affairs: one that most significantly tells us just how atypical a hominin *Homo sapiens* is (see Tattersall 2012).

Nonetheless, the underlying paleoanthropological disdain for systematics tenaciously persists, along with the associated minimalist mindset. Most obstructively, this desire to cling to the past expresses itself in the form of a numbing reluctance to recognize more fossil hominin species and genera than absolutely necessary. If we have to have more taxa, the reasoning seems to go, then let's at least have as few of them as possible. This minimalism has had generally insalubrious results that perhaps most unhelpfully include the remarkably durable pursuit of the "earliest *Homo*" launched by the description of *Homo habilis* (Tattersall 2015). This long-running grail-chase has led to the inclusion in our genus of a mind-boggling range of morphologies (and hence presumably of differentiated taxa), dating back now to 2.8 myr (Villmoare *et al.* 2015); and even if the resulting swollen "*Homo*" assemblage is monophyletic (not a sure bet), cramming everything into a genus perforce defined by *H. sapiens* has inevitably inhibited investigation of the substantial morphological and phylogenetic structure that lies within it. Indeed, every new addition to our genus has further impressed observers with the remarkable "variability" (hence lack of definability) of the genus – which has, in turn, made it easier to justify stuffing yet more morphologies into it.

MOLECULAR SYSTEMATICS AND PALEOANTHROPOLOGY

Things might have continued in this diffusely conflicted vein pretty much indefinitely, had not a radical innovation invited us to rethink questions of species-level diversity and divergence in paleoanthropology, at least during the most recent phases of human evolution. That innovation is, of course, the addition of the techniques of molecular genetics and systematics to the paleoanthropological arsenal. Until close to the turn of millennium, morphology (gross and microscopic) had supplied the sole legitimate criterion for species recognition in paleoanthropology – although it must also be admitted that in practice paleoanthropologists had far too frequently also allowed issues of geological age and geographical provenance to influence their judgment. But with the application of the methods of molecular systematics to the recent hominin fossil record the rules changed, at least for those fossils that satisfied the age and environmental requirements for the recovery of ancient DNA (aDNA). The resulting complexities have not yet been systematically thought through; but it is already clear that, going forward, the availability of genomic information both from fossils and from rapidly enlarging samples of modern humans will make it increasingly difficult for us to avoid confronting the issue of what the units actually are that we are perceiving and naming in the relevant part of the human fossil record, and what the biological attributes might be that actually delimit them.

The impact of genomics was not felt in paleoanthropology as immediately as it might otherwise have been, because when the first extraction of Neanderthal mitochondrial DNA (mtDNA) was achieved (Krings *et al.* 1997), the sequence reported was found to fall outside the range of variation of modern humans: a finding that fit well with the growing and long-overdue morphological consensus (see Tattersall 2009) that the Neanderthals represented a lineage entirely distinct from that of modern humans, with a common ancestry at some point over half a million years ago. In other words, the initial mtDNA findings suggested that, although closely related, the two hominins were completely differentiated. They were indeed different species, whatever that meant.

Since then, however, the picture has grown more complicated. Recovery of nuclear aDNA from a growing sample of late Pleistocene hominins has suggested that interbreeding between *Homo sapiens* and the resident *H. neanderthalensis* King, 1864 actually did take place in a number of areas of Europe and western Eurasia, early in the period of initial contact after the first sapiens had left Africa some 60 000–80 000 years ago (e.g. Villanea & Schraiber 2019). Remembering the key criterion (interbreeding) of the still-dominant Biological Species Concept (BSC) that Dobzhansky favored in 1944 and that was so vigorously promoted by Ernst Mayr, some have concluded from this hybridization that perhaps *Homo neanderthalensis* and *Homo sapiens* are not really distinct at all, because in some way the Neanderthals may "live on" in us, in the form of alleles scattered throughout the human genome that may be of Neanderthal origin (Ungar & Burakoff 2023; Wei *et al.* 2023) – although others have concluded the opposite, namely that Neanderthals fully qualify as a species under the BSC (White *et al.* 2014).

Complicating the matter yet further is a recent finding that some six percent of Neanderthal genes had already been acquired from a very early and now-extinct lineage of *Homo sapiens* (Harris *et al.* 2023). Add to inferences of this kind the identification of the distinctive Denisovan sister-lineage of the Neanderthals, first identified from DNA alone (Reich *et al.* 2010) and now reported to have introgressed both with modern humans and Neanderthals (Wolf & Akey 2018), and the detection of various "ghost lineages" (e.g. Rogers *et al.* 2020), some of them quite ancient and all known only from the genomic traces they have left in modern human populations around the Old World, and it is hardly surprising that some paleoanthropologists (e.g. Harvati & Ackermann 2022) have begun to muse once more about what Hennig (1966) called "tokogenetic" evolution. Evolution of this kind would have involved the "braided streams" of diverging and merging hominin populations and morphologies that were championed by Holliday (2003) in a wide-ranging review of species concepts as applied to our group.

However, it remains true that over the long haul the morphological structure we see throughout the evolutionary record has to have accumulated through the historical divergence of lineages; and all the past and present phylogenetic patterns we perceive today necessarily depend on the historical imprimatur imparted by irrevocable processes

of speciation and lineage-splitting. What is more, while braided-stream reticulating patterns undoubtedly occur regularly within primate species as intraspecific variants differentiate and recombine under the influence of climatic and topographic fluctuations, the two phenomena of divergence and reticulation are very different, not only in their mechanisms and levels of effect, but in their long-term consequences. Most importantly, the hierarchical structure we see in nature cannot result from a braided dynamic, which will by definition militate against speciation and historic individuation. As a result, in the case of recent members of the genus *Homo* (which is, or should be, a monophyletic set of very recently diverged and hence very closely-related lineages, among which some opportunistic hybridization might routinely be expected, circumstances permitting), the question arises of whether we are merely seeing the results of the intraspecific mechanisms that Ernst Mayr might have predicted, or whether we are observing true divergence and evolutionary innovation via speciation.

In the case of those members of our genus that are well differentiated morphologically, for example *Homo sapiens* and *H. neanderthalensis*, divergence is almost certainly implicated, not least because the extensive and paleontologically unanticipated differences between the two hominins in skeletal construction argue for a radical and ramifying developmental reorganization at the origin of the anatomically distinctive and highly apomorphic *H. sapiens*. The speciation event at issue took place at some point over 230 kyr ago (Vidal *et al.* 2022); and despite apparent genomic indications of hybridization between Neanderthals and moderns at early stages (Villanea & Schraiber 2019), that intermixing was evidently followed immediately by significant purifying selection against Neanderthal alleles (Currat & Excoffier 2011; Juric *et al.* 2016; Petr *et al.* 2019). On a broader scale, it is also evident that Neanderthal/modern encounters did not materially change the established evolutionary trajectories of either lineage: the Neanderthals rather rapidly went on to become extinct identifiably as themselves, whereas *Homo sapiens* went on to take over the world pretty much as it would certainly have otherwise done, with or without the odd advantage or handicap conferred by a handful of genes that might have been recently acquired from Neanderthals or Denisovans. There is no convincing signal anywhere of biologically meaningful lineage re-coalescence.

Like the BSC, most currently accepted definitions of the species in biology rely in one way or another on reproductive continuity among populations, or on reproductive discontinuity between them. But it is always necessary to keep in mind that fine boundaries in nature are often blurred, and that the processes involved in speciation do not necessarily give rise to instant total discontinuity. A recent review by Cortés-Ortiz *et al.* (2019) makes it clear that recently differentiated primate lineages in secondary contact may often display hybridizing behaviors that do not lead to long-term integration; and Ernst Mayr himself (e.g. 1963) emphasized how isolating mechanisms frequently need themselves to evolve (as we apparently see happening among

modern humans and Neanderthals). What is important in determining whether speciation has occurred in any particular case is thus not hybridization itself, but whether the hybridizing lineages were or are reintegrating or not. This is often difficult to determine for living species, but it should be more readily visible in the coarser grain but greater temporal perspective that the fossil record supplies. And if one subscribes to the reasonable proposition that a fossil species is a morphologically (and/or perhaps genomically) recognizable lineage that has embarked on its own unique and irreversible evolutionary trajectory, a viewpoint fully compatible with the paleontologist George Gaylord Simpson's (1961) "Evolutionary Species Concept", there can be little doubt that *Homo neanderthalensis* and *Homo sapiens* were indeed fully differentiated species, and that they merit recognition as such.

Whether the same can yet be said for any of the lineages within *Homo* that were initially identified purely on molecular grounds, is less evident. The Denisovans have not so far been associated with any useful or definitive morphologies, and the genomicists who identified the unique Denisovan molecular signature have been wise enough to retain a purely informal nomenclature for the group. Even now, the evidently once widely distributed Denisovans are so poorly known morphologically that it is anyone's guess how many Denisovan individuals might already be recovered and resting on museum shelves, identified as Neanderthals or as something else. This will obviously be a big issue for the future. And of course, those lineages for which we have no hints in the fossil record, and whose existences are entirely inferred from the DNA traces they left in the various hominins with whom they putatively interbred, must remain entirely conjectural and without any kind of physical or cultural identity. As genomic algorithms improve, we may find ourselves obliged to acknowledge that many such lineages were out there in a formal sense; but without knowing more about them, and particularly about their fates, we cannot meaningfully incorporate them into any narrative of human evolution. What they do very strongly hint, however, is that there was a great deal more hominin diversity in the later Pleistocene (and quite plausibly earlier) than analyses of the fossil record have so far led us to suspect. And perhaps one of the most salutary effects of the introduction of molecular information into paleoanthropology will be to send us back to look at the fossils and their contexts in finer grain.

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