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The development of ideas about a recent African origin for *Homo sapiens*

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Summary - In this contribution I will review the development of ideas about a recent African origin for our species over the last 50 years, starting from the time of my PhD in the early 1970s. I will examine the instructive and quite different interpretations placed on the 1979 discovery of a partial Neanderthal skeleton associated with a Châtelperronian industry at the rock shelter of St-Césaire in France, and then focus on the crucial years from 1987-1989, including the so-called 'Human Revolution' conference of 1987, and my 1988 Science paper with Peter Andrews: 'Genetic and Fossil Evidence for the Origin of Modern Humans'. Following the historical review, I will assess the status of five proposed models for the evolution of derived Homo sapiens: Recent African Origin (RAO); RAO and Hybridisation (RAOH); Assimilation (AM); Multiregional Evolution (MRE); and Braided Stream (BS). I conclude that a recent African origin model with hybridization (RAOH) is the best supported from the fossil and genetic evidence.

Keywords - Africa, Homo sapiens, Evolution.

Introduction

Those of us researching in the field of palaeoanthropology during the last two decades have been privileged to witness a period of dynamic, even revolutionary, growth in our knowledge of recent human evolution. In this review I would like to take an even longer view of the development of ideas about an African origin for our species, start-ing from the time of my PhD in the early 1970s, with a focus on the crucial years from 1987-1989, including the so-called 'Human Revolution' con-ference of 1987, and my 1988 "Science" paper with Peter Andrews: 'Genetic and Fossil Evidence for the Origin of Modern Humans', which is still my most highly cited publication (Stringer and Andrews 1988). In this paper I will also circumvent one of the most troublesome problems in discussing our origins - the terminology around "archaic" and "modern" humans - by using the alternative informal descriptive terms "basal" and "derived" to delineate evolutionary change within both the H. sapiens (bHs and dHs) and H. neanderthalensis (bHn and dHn) lineages (as discussed in Stringer and Crété 2022). These terms are, of course, subjective but certainly no more so than labels like archaic, anatomically modern, and behaviourally modern. However, I can point to morphologies and phylogenies that illustrate the division, such as the contrast between Omo 2 and Irhoud (basal) and Skhul and Qafzeh (derived) in endocranial shape (e.g. Neubauer et al. 2018), and phylogenetic position (e.g. Ni et.al. 2021).

Models for the evolution of derived *H. sapiens*

I will now summarise some of the main current models for the origin(s) of dHs (adapted from Stringer 2014), with the addition of a fifth model (the braided stream) that is currently gaining some usage. I will return to a discussion of these models after I have reviewed earlier ideas about the origin of our species.

(i) **the Recent African Origin model (RAO)** argues that derived *H. sapiens* (dHs) evolved in Africa during the last ~500,000 years and spread from there throughout the world. Indigenous populations in other areas of the world were

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replaced by the dispersing groups, with little, if any, hybridisation between the groups.

(ii) the **RAO and Hybridisation model** (**RAOH**) is similar to the above, but allows for a greater extent of hybridisation between the dispersing populations and the resident indigenous populations outside of Africa.

(iii) the **Assimilation model (AM)** accepts a predominantly African origin for dHs. However, it differs from the previous models in denying replacement or population dispersion as the main process in the appearance of dHs around the world. Instead, this model emphasises the importance of demic diffusion, admixture, changing selection pressures and resulting directional morphological change in the areas where dHs appeared.

(iv) the **Multiregional Evolution model** (**MRE**) differs from the previous three in denying a recent and primarily African origin for dHs. It emphasises the role of both genetic continuity over time and gene flow between contemporaneous populations in arguing that dHs evolved from their early Pleistocene forebears not only in Africa but in every inhabited region of the world.

(v) The **Braided Stream model (BS)** argues that human evolution across the Pleistocene inhabited world can be represented as a stream consisting of multiple larger or smaller channels that divide and recombine, forming a pattern resembling the strands of a braid. The smaller streams represent evolutionary events that separate populations, gene pools, or lineages from each other. In time they either go extinct or reunify into the common gene pool leading to dHs globally. For example, China has been described as a region that 'represents one stream of the intertwining river of evolutionary change that flows over all areas of the globe where human habitation occurred' (Rosenberg and Wu 2013).

1970-1984

In writing this historical overview, it is first necessary to transport us all back to the time when I began my PhD, one which concentrated on the relationship between Neanderthals and *H. sapiens*

(see also Stringer 1994, 2014) but one where none of the five models for the origins of H. sapiens summarised above had yet been articulated and named. In 1970 the intellectual environment of palaeoanthropology had unilinear gradualism at its heart, and the term H. sapiens often encompassed fossils as morphologically diverse as those from Cro-Magnon, La Ferrassie, Kabwe and Ngandong (Campbell 1963). Material culture and morphology as recorded in the fossil record were often thought to have evolved in concert, with innovations in behaviour directly influencing evolutionary changes in anatomy, for example in the brain or the dentition (Brace 1967; Brose and Wolpoff 1971). There was a further major limitation that was hardly recognised at the time - there was little meaningful way to reach beyond the direct or indirect application of conventional radiocarbon dating to the fossil and archaeological records of the Pleistocene, except for the rare cases where volcanic deposits could be used for calibration. With its inevitable (but then unrecognised) compression of time, this limitation prevented the provision of a realistic chronology for the fossil human and archaeological records of the middle-late Pleistocene, particularly in Africa, Asia and Australasia.

From my work on British Quaternary sites in the mid-late 1970s (Stringer 2006), I was familiar with the European glacial-interglacial framework that allowed a rough ordering of the archaeological and palaeontological records of the continent (Cook et al. 1982). Using that framework, Europe seemed to be the only continent with a reasonably stretched post-erectus chronology, including fossils like Mauer, Arago and Swanscombe, that appeared to date between about 500- 250 ka, and I was fairly confident from my and William Howells' work that Europe contained Neanderthals and their ancestors, not the ancestors of dHs (Howells 1974; Stringer 1974, 1978). However, the enigmatic early Upper Palaeolithic Châtelperronian industry in France seemed to have evolved out of the locally preceding Mousterian of Acheulian tradition about 35,000 years ago, leaving open the possibility that a parallel in situ evolutionary transition from Neanderthal-dHs had occurred (Brose and Wolpoff 1971), that undiscovered dHs were in fact responsible (as suggested by Bordes 1968), or that Neanderthals were actually the manufacturers, which I considered possible (see below).

One of the most significant finds in progressing this question was the partial Neanderthal skeleton found in Châtelperronian (early Upper Palaeolithic) levels at St-Césaire, France, in 1979 (Lévêque and Vandermeersch 1980). This discovery was noted by ApSimon, who wrote a commentary on its significance for the journal "Nature" the following year (ApSimon 1980). In the 1974 summary of my thesis results (Stringer 1974), I had postulated that the Châtelperronian could have been made by Neanderthals, echoing the views of Richard Klein (Klein 1973a), but ApSimon's interpretation of the find seemed odd to me, since he appeared to argue that it complicated the Neanderthal-dHs transition, and provided support for population continuity. In contrast, I thought the discovery clarified the situation in Europe by demonstrating polyphyletic origins for what was called the Upper Palaeolithic, and a clear demarcation between late Neanderthals and the dHs who had apparently produced the contemporaneous Aurignacian. Accordingly, together with Robert Kruszynski and Roger Jacobi, I wrote a critical reply to ApSimon's piece, and this was published, with a quite different reply by Milford Wolpoff, and ApSimon's response in 1981 (Wolpoff et al. 1981a).

This discovery catalysed the debate about events in Europe around the Neanderthal-dHs transition, though initially not at all in the way I expected. I corresponded with a number of other researchers over its significance, exchanging views as different as Wolpoff's (who argued that the find strongly supported local technological and morphological evolution from Neanderthal to dHs populations) and Bordes' (Bordes 1981) who argued in a letter to me that the skeleton represented a victim of the *H. sapiens* manufacturers of the Châtelperronian, who had considerately given him a decent burial! (see Tab. 1). Reading archaeological commentaries around the time is both instructive and sobering as Tab. 1 - Different schema to explain theNeanderthal-Châtelperronianassociation atSt-Césaire (1981).

CULTURE/ AUTHOR	WOLPOFF	BORDES	STRINGER
Aurignacian	H. sapiens	H. sapiens	H. sapiens
Châtelperronian	Transitional	H. sapiens	Neanderthal
Mousterian	Neanderthal	Neanderthal	Neanderthal

many took the position summarised by (White 1982): "if there is a relationship between culture and biology across the [Middle-Upper Palaeolithic] boundary, cultural developments... are stimulating biological change rather than vice versa". To my surprise, then, rather than challenging the fundamentals of biological continuity, the association of a Neanderthal with the Châtelperronian seemed for a while to instead reinforce the models of Brace (1967) and Brose and Wolpoff (1971) that technological change (or perhaps social change) was catalysing evolutionary trajectories towards dHs. My response, influenced both by an analysis I had recently completed with Erik Trinkaus on the Shanidar crania (Stringer and Trinkaus 1981) and by my frustration with the debate, was to write a polemical and cladistics-based paper in the "Journal of Human Evolution" (Stringer 1982). This seemed to have little or no impact on the situation, but at least served to usefully focus my views on the Neanderthals for the next phases of my research.

The European transition from Neanderthals and their associated Middle Palaeolithic tools to dHs and the associated Upper Palaeolithic was believed from radiocarbon dating of fauna and charcoal to have occurred about 35,000 years ago. But because of dating limitations, the nature and extent of evolution or overlap between these taxonomic and archaeological units could not be determined. Elsewhere, there seemed to be a dearth of informative material in the appropriate timeframe, with few realistic alternative ancestors Tab. 2 - Supposed correlations of technological'stages' between Europe and Africa 1975 vs 2022.

EUROPE	AFRICA (1975)	AFRICA (2022)
Upper Palaeolithic	Middle Stone Age	Later Stone Age
Middle Palaeolithic	Early Stone Age	Middle Stone Age
Lower Palaeolithic	Early Stone Age	Early Stone Age

for H. sapiens from Africa, or anywhere else for that matter. In the Levant, a similar transition period from Neanderthals to H. sapiens was believed to lie only slightly beyond this 35,000-year-old watershed. Even as late as 1985 it was believed by most workers, including me, that the pattern of population change in this area followed that of Europe, or rather preceded it, by only a small amount of time. Thus Neanderthals at Israeli sites such as Tabun and Amud evolved into, or gave way to, early dHs such as those known from Skhul and Qafzeh by about 40 ka (e.g. see Trinkaus 1984). For some workers (following Clark Howell's ideas: Howell 1957; Jelinek 1982) there had been interlinked technological and biological changes, leading to the evolution of dHs in the region from "generalised" Neanderthals, and it was postulated that they then migrated into Europe, giving rise to the populations associated with the Upper Palaeolithic.

In Africa, the Lower Palaeolithic was generally believed to have continued until about 50 ka, while the local transition from the Middle Stone Age (technologically equivalent to the Middle Palaeolithic) to the Later Stone Age (technologically equivalent to the Upper Palaeolithic) was generally believed to date from an even younger time than further North, perhaps as recent as 12 ka (Clark 1970). Thus the African Lower Palaeolithic supposedly spanned the timescale of the Lower and Middle Palaeolithic of Europe, while the Middle Stone Age was only temporally equivalent to the European Upper Palaeolithic (Tab. 2). Hence African cultural and physical evolution was thought to have lagged considerably behind that of Europe and western Asia, and this was reinforced by the belief (from radiocarbon

dating) that plesiomorphous humans such as Florisbad and Jebel Irhoud dated from only 40 ka or 50 ka, and the even more plesiomorphous Kabwe cranium from only about 125 ka (Klein 1973b). Thus while I thought estimates for the age of the Omo Kibish material of at least 100 ka were plausible (Leakey et al. 1969), I placed fossils like Kabwe and Elandsfontein at about the same age as Omo, while Jebel Irhoud 1, as mentioned, seemed to be younger still.

In East and Southeast Asia, the pattern of human evolution was even more difficult to discern in the 1970s. Some Asian fossils such as those from Zhoukoudian Lower Cave (and their associated stone industries) were dated via correlation with European glacial-interglacial sequences as far back as 400 ka, but Brace's influential view that fossils such as Maba and Ngandong were representatives of a Neanderthal stage in our evolution meant that these, too, were often dated to the equivalent of the last glaciation, while fossils like Wajak were seen as transitional or "Neandertaloid" (Brace 1967). However, there was evidently a significant gap before the appearance of unequivocally dHs in the Far East. Until the first radiocarbon dating of the Mungo material in the 1970s, it was believed that the arrival of humans in Australia was a very late event, dated at perhaps 10-15 ka (Howells 1967). With the possible age of Mungo moving back towards 30 ka (Bowler and Thorne 1976), and the Niah Cave material tentatively dated at about 40 ka (Harrisson 1970), the apparent gap between more plesiomorphous fossils and dHs narrowed. But even accepting Omo Kibish 1 as the oldest known dHs, I was unable to construct a credible model for the evolution of our species during the 1970s, because of confused intercontinental chronologies as well as the lack of plausible African ancestors for the Omo Kibish population in the right time frame.

Even up to 1984, prevailing views on recent human evolution were either that there was a geographically widespread emergence of *H. sapiens*, or that origin took place in a region outside of the African continent. However, things started to change in that year, when two important

volumes on human evolution were published. The two publications centered on H. erectus, the putative ancestral form for H. sapiens (Andrews and Franzen 1984), and on the origins of H. sapiens itself (Smith and Spencer 1984). The authors included a new generation of students who were prepared to look at the evidence and the prevailing views in novel and sometimes challenging ways. The Andrews and Franzen volume actually ranged much more widely than discussions of *H. erectus*, and contained some of the first applications of cladistics to recent human evolution, but it also contained a chapter by Bräuer on the possible African origins of H. sapiens (Bräuer 1984a). The Smith and Spencer volume had chapters covering four broadly defined geographical regions: Europe, Africa, western Asia, and East Asia. Europe was divided into western and central areas with contrasting conclusions, mine with Hublin and Vandermeersch presenting a replacement scenario for western Europe (Stringer et al. 1984) with the possibility of an African source for *H. sapiens*, while Smith (1984) argued for regional continuity in eastern Europe, something also proposed by Trinkaus (1984) for western Asia. For Africa, Bräuer (1984b) further developed his Afro-European sapiens hypothesis, while Rightmire (1984) also favoured an early emergence of sapiens morphology in Africa, but was more cautious about wider extrapolations. Wolpoff, Wu, and Thorne (1984) provided the first detailed presentation of multiregional evolution, focusing on the fossil material from East Asia and Australasia and arguing for specific anatomical connections between fossils from China and Java generally assigned to H. erectus and extant peoples in those regions today.

Our contribution to the Smith and Spencer volume considered the evolutionary position of fossils like Swanscombe and Steinheim (Stringer et al. 1984). Earlier discussions of the European hominin sequence tended to argue for either a parallel evolution of Neanderthal-like and *sapiens*-like forms (the 'presapiens model' of workers like Boule and Vallois, 1952) or unilinear gradualism leading through a Neanderthal stage to dHs (following researchers like Hrdlička 1930, and Brace 1967). While the Swanscombe and Steinheim fossils were recruited to support each of those models, the late 1970s and 1980s saw growing recognition that these could represent Neanderthal, not *sapiens* ancestors as part of an accretional appearance of Neanderthal characteristics during the Middle Pleistocene (e.g. Stringer 1974,1978; Hublin 1983,1988). But the seemingly parallel transition from Neanderthal/Middle Palaeolithic samples to dHs/Upper Palaeolithic could be interpreted through the lens of evolutionary continuity or population replacement.

1985-1989

It may seem now that conferences make little impact on the progress of science, apart from providing networking opportunities. This is undoubtedly largely due to the long lead-in time for the planning of conferences, compared with the increasingly rapid dissemination of new data, particularly through electronic media. But in contrast, in the period from 1970-1990, conferences were often venues for the first presentation of new data and analyses. The fossil material itself was the subject of the "Ancestors" meeting and exhibition held in New York in 1984, and the papers from the meeting formed the basis of an influential volume published the following year (Delson 1985). From this time onwards, the appearance of modern humans was increasingly recognized as a real evolutionary event, perhaps even a speciation event, and the importance of Africa in that process was also increasingly acknowledged. However, in 1985, genetic data were still making negligible impact on reconstructions of modern human origins, something that was to change dramatically in the next three years. Two further meetings that I attended profoundly influenced the following few years of my scientific research, and I believe they similarly affected other participants: the Santa Fe Advanced Seminar "The Origins of Modern Human Adaptation" organised by Erik Trinkaus in 1986, and the Cambridge Origins and Dispersal of Modern Humans meeting organised by the late Paul Mellars and me in the following year. The former meeting, with contributed papers was eventually published in 1989 (Trinkaus 1989), and brought together workers such as Lew Binford, Milford Wolpoff and Ofer Bar-Yosef in a small, closed workshop, with papers pre-submitted and circulated, rather than presented. Thus discussion time was maximised, and it was originally intended that the recorded and transcribed workshop proceedings would be published alongside revised versions of the submitted papers - an idea that was abandoned because of the discursive and confrontational nature of some of the initial exchanges. Nevertheless, over three days, I got a much better (and overall constructive) insight into the thinking of Palaeolithic archaeologists than I had managed over many previous years.

A year later, in 1987, one of the first applications of emerging chronometric techniques (thermoluminescence applied to burnt flint) heralded several new approaches to calibrating palaeoanthropological sites beyond the range of radiocarbon. The first result seemed to reinforce the expected pattern in the Levant, dating the recently discovered Neanderthal burial at Kebara in the anticipated time range of about 60 ka (Valladas et al. 1987). However, shortly afterwards, the first application was made to the site of the Qafzeh early dHs material (Valladas et al. 1988), giving a surprising age estimate of about 90 ka, more than twice the generally expected figure, but in line with earlier suggestions made by Farrand from geology (Farrand 1979), and Tchernov from biochronology (Tchernov 1981), and cited by Bar-Yosef and Vandermeersch (1981). Further applications of non-radiocarbon dating methods later amplified the pattern suggested by the age estimates for Qafzeh and Kebara (e.g. see Grün and Stringer 1991). It seemed likely that the early dHs burials at both Qafzeh and Skhul dated to between about 90-130 ka, while the Neanderthal burials from Kebara and Amud dated younger than these figures, in the range 50-60 ka. This newly emerging chronology meant that scenarios of unilinear

evolution from Neanderthals to dHs in both the Levant and Europe started to be reassessed. Some of us heightened efforts to try and identify alternative origins for the Skhul and Qafzeh people, whether from local predecessors such as Zuttiyeh, or from further south, in Africa. As the intervening period between the Levantine early dHs and Neanderthals approximated the transition from "interglacial" Marine Isotope Stage (MIS) 5 to "glacial" MIS 4, this also led to a proposed scenario where Neanderthals only appeared in the Levant after the onset of glaciation further North (Bar-Yosef 1998). However, direct dating of the Tabun C1 specimen now suggests that this Neanderthal could date from around the MIS 5-6 boundary (Grün and Stringer 2000).

The emergence of these important new chronologies for the Levant coincided with the 1987 Cambridge meeting, which was on a much larger and more public scale than the Santa Fe workshop of a year earlier, and also witnessed many of the biggest names in palaeoanthropology coming to grips with rapidly developing data and ideas from palaeontology, archaeology and genetics. This was set against the growing contest between Multiregionalism (MRE) and Recent African Origin (RAO) that was to dominate debate for the next fifteen years or so (Stringer 2002). Mellars and I described the difficult gestation of what became known as the Human Revolution meeting in our introduction to Volume 1 of the conference papers (Mellars and Stringer 1989a,b), but I think the meeting achieved its academic aims (e.g. see Lewin 1987), and set a number of research agendas for the following decade.

From now on, many of those research agendas would include a consideration of genetic data on the origin of *H. sapiens*. Although palaeontological and archaeological discoveries had been pushing a small but growing community of researchers in the direction of a RAO or RAOH model for *H. sapiens*, there is no doubt that, for better or worse, it took the "Nature" paper by Cann et al. (1987) to reinforce the central importance of Africa for the origins of *H. sapiens* in particular, as well as for hominin origins



in general. Earlier studies had to work with population frequencies of genetic markers, the products of the genetic code (e.g. blood groups, proteins) and by combining data from populations, attempts were made to reconstruct the genetic history of humans (Cavalli-Sforza and Bodmer 1971; Nei and Roychoudhury 1982). However, the advent of techniques that revealed individual molecular sequence data allowed phylogenetic trees or genealogies of specific genes or DNA segments to be constructed. Two pioneering papers published in "Nature" in 1986 and 1987 heralded the genetic revolution to come. One was population frequency-based, while the other adopted a phylogenetic approach using DNA markers called Restriction Fragmentation Length Polymorphisms. In the 1986 paper, Wainscoat et al. (1986) studied polymorphisms close to the beta-globin gene, and showed by genetic distance analyses that African populations were quite distinct from non-African ones, which in turn shared features with each other. They concluded 'it has been argued that the evolution of modem man took place in Africa. Our data are consistent with such a scheme, in which a founder population migrated from Africa and subsequently gave rise to all non-African populations'. A year later, Cann et al. (1987) produced a genealogy of 134 mitochondrial DNA variants derived from restriction maps of 148 people from different regions. The genealogy was used to reconstruct increasingly ancient hypothetical ancestors, culminating in one female, most parsimoniously located in Africa. Moreover, using a mtDNA divergence rate calculated from studies of other organisms, it was estimated that this hypothetical female ancestor lived ~200 ka ago. These conclusions were extremely controversial and were accompanied by much media hype, and they were soon challenged from various directions, including during fierce debate at the Cambridge conference. Because I was privileged to be centrally involved in that meeting, its discussions provided a crucial framework for the "Science" paper that Peter Andrews and I started to assemble in the same year (Stringer and Andrews 1988).

As we said in the opening paragraph of 'Genetic and Fossil Evidence for the Origin of Modern Humans': 'We examine two opposing models [MRE and RAO] proposed to explain the origin of Homo sapiens and compare their compatibility with recent reviews of genetic and paleontological data. These two models are not the only ones currently under discussion, but it is likely that one or other reflects the predominant mode of Homo sapiens evolution. Comparison of these two extreme models should allow the clearest tests for the models from existing data, tests which are not feasible for several other proposed models' (Stringer and Andrews 1988). These tests were summarized in table 1 of the paper, reproduced below (Tab. 3), and we argued that our assessments favoured RAO over MRE for each aspect, while recognizing that fossil and archaeological data from Europe, Southwest Asia and Africa provided clearer support than did the more contentious records of eastern Asia and Australasia. In our view, the growing body of genetic data also predominantly supported RAO over MRE, although those data were only the tip of a large iceberg that continues to emerge to this day, and that support is now less absolute than would have been predicted from the mtDNA analyses alone.

Our conclusions were also tempered by a recognition of the importance of the western Asia record to the story: "Although we feel that an African origin for Homo sapiens is highly probable, the exact time, place and mode of origin of the species cannot yet be determined. The presence of Homo sapiens fossils in the early part of the late Pleistocene at both the southern tip of Africa and in the Levant means that a southern African origin as recent as 100,000 years ago is unlikely. The origin of the species must have been more ancient, and, as we have seen, plausible precursor populations arc sampled at sites in northern, eastern, and southern Africa. Given the recently determined age of the Qafzeh Homo sapiens fossils, even the adjacent area of the Levant cannot be excluded as a possible source area for Homo sapiens. However, it appears that only the genetic divergence and diversity of subSaharan African

ASPECT	MULTIREGIONAL EVOLUTION	RECENT AFRICAN EVOLUTION
Geographic patterning of human evolution	Continuity of pattern from Middle Pleistocene to present	Continuity of pattern only from late Pleistocene appearance of <i>H. sapiens</i> to present
	Interpopulation differences are high, greatest between each peripheral area	Interpopulation differences relatively low, greatest between African and non-African populations
	Intrapopulation variation greatest at centre of human range	Intrapopulation variation greatest in African populations
Regional continuity and the establishment of <i>H.</i> <i>sapiens</i>	Transitional fossils widespread	Transitional fossils restricted to Africa, population replacement elsewhere
	Modern regional characters of high antiquity at peripheries	Modern regional characters of low antiquity at peripheries (except Africa)
	No consistent temporal pattern of appearance of <i>H. sapiens</i> characters between areas	Phased establishment of <i>H. sapiens</i> suite of characters: (i) Africa, (ii) S.W. Asia, (iii) other areas
Selective and behavioural factors involved in the origin of <i>H. sapiens</i>	Factors varied and widespread, perhaps related to technology; local behavioural continuity expected	Factors special and localised in Africa; behavioural discontinuities expected outside Africa

populations now reflect an age appropriate for the species origin, presumably because areas of northern Africa and the Levant have been exposed to extensive subsequent gene flow from Eurasian populations, particularly in historic times".

Andrews and I acknowledged that we were not testing all the possible models of H. sapiens origins, although Bräuer's RAOH was cited, as were Smith and Trinkaus's developing views that would lead to AM (Trinkaus 1984; Smith, 1984). However, Smith was a signatory to a highly critical reply to the 1988 paper (Wolpoff et al. 1988), which argued 'The recent article by Stringer and Andrews on the origins of modern humans confounds rather than clarifies the issues...it contains contradictions, misrepresentations, and omissions and is a step backward from the progress made during what has been anything but "a period of relative neglect." The value of their dichotomy, even as a heuristic device, is undermined when they then assume the hypothesis they set out to test, through their initial contentions that the origin of modem

humans is "an event" and that modem humans are a new species distinct from earlier "archaic" populations of *Homo sapiens*'. We replied that 'we had hoped that the reaction to our article from supporters of the multiregional model would be based on the presentation of further data to test the models. We look forward to such a constructive response from those who signed the letter by Wolpoff et al.' Unfortunately the following years did not witness constructive engagement between the two factions in the debate, a situation that persisted for more than two decades (Gibbons 2011).

Revisiting the models

Regarding the current status of the five models summarised at the beginning of this contribution, I consider that both a strict RAO and MRE as presented in the late 1980s and 1990s have been falsified (Stringer 2014). There are enough genetic data to show that while extant populations can be described as more than 90% RAO from their genomes, the figure is not close to the 100% expected from the complete replacement of non-Hs lineages outside of Africa. Equally, I strongly doubt that any palaeoanthropologist would now argue that indigenous Australians show 'the mark of ancient Java' in the manner argued by prominent multiregionalists (Wolpoff et al. 1984), and I hope that they would no longer argue that the Sangiran 17 *H. erectus* cranium was actually 'a great big hyper-robust Australian aborigine' (M. Wolpoff, quoted in Shreeve 1995, p.102).

However, ideas of regional continuity have remained strong in China (Cheng 2019). For example Rosenberg and Wu (2013) stated 'It is our contention that the currently existing human fossil record in China shows evidence of continuity of what have been described as East Asian features in the cranium, dentition, and occasionally in the less often represented postcrania that suggest a gradual rather than an abrupt trend toward modernity in East Asia...these features do not appear all at once as a "package of modernity" but as an evolutionary mosaic that is consistent with the gradual transition of a population through time and that is not consistent with replacement by an outside population'. In a more recent article Wu et al. (2021) go even further in arguing that the morphology of the Hualongdong 6 cranium indicates that China was itself a location for the origins of dHs: 'Both the number of its modern facial features and their pronounced expressions in HLD 6 exceed those of all other late Middle Pleistocene hominin crania currently known from China. This would suggest that the transition from archaic to modern morphology in eastern Asia occurred earlier than current convention dictates, possibly as early as 300 ka. In addition, the HLD 6 partial cranium, with its multiple derived modern facial features, suggests not only that its population included the earliest transitional member linking morphologically archaic and early modern humans in the region but also that the initial transition to modernity happened in some isolated regions of China while more archaic hominins contemporaneously occupied other areas'.

Such ideas lacks proper consideration of the phylogeny of the so-called 'modern' face, in which many traits are actually plesiomorphous (Lacruz et al. 2019), while others may be homoplasies (that is, not in the common ancestor but evolved independently afterwards) between dHs and the Chinese lineage containing the fossils from Dali, Hualongdong and Harbin (Ni et al. 2021). They also lack any meaningful engagement with the extensive relevant genetic literature (e.g. Bergström et al. 2021; Liu et al. 2021; Mao et al. 2021) that so far indicates no deep connections between ancient Chinese populations and those of today, except where those ancient Chinese populations might be related to Denisovans.

Concluding remarks

In my view, the years from 1970-1990 advanced palaeoanthropological thinking on dHs origins more than any other two decades in the last century, although it will need historians of science to provide a more objective opinion on that than I can. These years saw substantial progress in our ability to calibrate the most recent stages of human evolution. Some specimens, such as late Neanderthals, had their estimated ages broadly confirmed, while others such as the early dHs remains from Skhul and Qafzeh, were shown to be much older than generally believed. In the archaeological arena it became increasingly clear that at least some African Middle Stone Age sites, and in some cases their contained human fossils, were much more ancient than had been believed (Tab. 2). A number of important new fossil discoveries were made, such as the partial Neanderthal skeleton from Kebara (Rak et al. 1983), and the late Neanderthals from Vindija (Wolpoff et al. 1981b) and St-Césaire (Lévêque and Vandermeersch 1980). The former two provided important information on Neanderthal variation, while the latter find allowed the enduring mystery of the makers of the Châtelperronian to be addressed with hard data at last (Tab. 1). Further finds and improved chronological control started to provide new

data about dHs dispersals into Australasia, showing an arrival on a comparable timescale to that being recorded in Europe, but all such developments were dramatically impacted by emerging genetic data near the end of the time period in question. Archaeological and palaeontological science would have continued to build an African origin scenario without "Mitochondrial Eve", of course, but it would have taken a lot longer to achieve wider acceptance for RAO/RAOH scenarios without the complementary genetic data to catalyse the debate.

Regarding the current status of models for the origins of dHs, the growing body of genetic data as well as new fossil and chronological evidence have modified how they fit the fossil record, and the appearance of dHs traits in Africa has moved further back in time than could have been envisaged in Stringer and Andrews (1988). There is also the recent addition of another model to consider - the Braided Stream. Personally I find it difficult to distinguish between the MRE and BS models, since both seem to feature regional continuity and reticulation across much of the range of Pleistocene humans, and as with MRE, such models applied to the Chinese fossil record (e.g. Rosenberg and Wu 2013; Wu et al. 2021) need to acknowledge the overwhelming predominance of Africa in the genomic and morphological origins of dHs. Certainly the Denisovan lineage contributed small amounts of DNA to the ancestry of extant East Asians after about 60 ka, but the wider and deeper morphological and genetic connections with more ancient Asian fossils expected from MRE and BS have not been detected so far (e.g. see Ni et al. 2021; Mao et al. 2021). If 'a river runs through' the Chinese record for the evolution of H. sapiens (Rosenberg and Wu 2013) it certainly seems to be a river of African origin, so perhaps braided stream from Africa (BSFA) might be more appropriate? AM does recognise the predominance of Africa in the process of *H. sapiens* evolution, but I would argue that the main dispersal phase of dHs seems not to show gradual regional morphological change outside of Africa under the influence of gene flow. While the associated genetic data

indicate gene flow from non-Hs populations into dHs (as expected from RAOH), there is not (so far) the reverse demic diffusion from dHs into indigenous populations outside of Africa expected from AM (Stringer and Crété 2022). As Galway-Witham and Stringer (2018) put it, under AM 'genes would have flowed gradually between these regional populations, catalysing genetic and anatomical changes and leading to the spread of modern traits. In contrast, RAOH envisages H. sapiens genes as largely entering and traversing Eurasia within the bodies of dispersing humans of African origin. Along the way there were successful hybridization events with indigenous populations, but these were effectively absorbing fragmented populations of indigenes in a relatively rapid replacement process, where they overlapped'.

I will end this review of more than 50 years of debate about our origins by saying that if data continue to show that the genetic and morphological ancestry of *H. sapiens* is more than 90% African then in my view RAOH best describes the overall process for the establishment of our species. For those who prefer not to use the model names I have employed here, then Svante Pääbo's neat summation should suffice: we are 'Mostly Out of Africa'.

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Author contribution

CS wrote this contribution.



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