

The evolution of the anatomically modern or advanced *Homo sapiens*: time, place, process, affinities and variations

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ABSTRACT

This paper surveys the opinions expressed in the recent literature on the origins of the anatomically modern *Homo sapiens*, and reviews the evidence from cranial and dental morphology argued by proponents of opposing views to support their case. It also critically analyses problems facing the interpretation of the evidence in arriving at a definitive conclusion to the debate.

Keywords: cranial morphology, dental morphology, Eve theory, *Homo sapiens*, human evolution, modern *Homo sapiens*, multiregional continuity, Out-of-Africa theory

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INTRODUCTION

For several decades, a major conflict has raged between two diametrically-opposed theories on the origins of *Homo sapiens*: the “Eve” or “Out of Africa” theory, and “multiregional continuity”. According to the Eve theory, the modern human species originated in Africa about 200 ka ago and spread out across the rest of the world. The anatomically-modern *Homo sapiens* replaced the archaic species of *Homo*, which had previously inhabited the various locations of the world, and thus the regional characteristics that can be observed among people today evolved following the worldwide spread of *Homo sapiens*. Multiregional continuity, on the other hand, holds that the regional differences between modern people reflect their ancestry from very early, regionally-established populations of *Homo erectus*. It accepts that all modern humans share similarities with one another that are not shown by any *Homo erectus*, but attributes these similarities to the progressive transformations that have occurred during the process of human evolution.

The origins of the debate lie in the work of Weidenreich and Coon, who focused on the extensive fossil record of the *Homo erectus* recovered between the 1890s and 1940s in Java and China.^(1,2) They argued that the modern Chinese

have evolved directly from the *Homo erectus* in China, whereas Australian Aborigines have descended from the Javanese *Homo erectus*. Coon’s theory, which can be called multiregional evolution, explains the morphological variation between fossil and modern human crania in terms of genetic isolation and differing rates of evolution. The re-expression of Coon’s theory in terms of multiregional continuity can be observed in the work of Wolpoff et al.⁽³⁾ Like Coon, they have overlooked any suggestion that anatomically-modern *Homo sapiens* dispersed from Africa, and instead assume that the races of *Homo sapiens* have evolved directly from their middle Pleistocene ancestors established in their respective geographical regions of Eurasia. Morphological differentiation is the product of a number of evolutionary processes, including the ancient establishment of regional characteristics, the maintenance of adequate and balanced gene flow across the Old World, selection pressures to adapt to local climatic conditions, and genetic drift. For example, in Australasia, a line of ancestry can be traced from the middle Pleistocene Java *Homo erectus*, through the late Pleistocene Lake Mungo and other Willandra Lake human fossils in Australia, to modern Australian Aborigines.

There are also some intermediate theories, which propose a greater role for Africa than is accepted by the multiregional continuity theory, and also allow for some genetic incorporation of archaic Eurasian populations. African hybridisation model: This is a modified version of the Eve theory proposed by Brauer as well as Brauer and Rimbach.^(4,5) According to this theory, the origins of modern humans are in Africa, but there followed a complicated hybridisation between the emigrants from Africa and the archaic populations of Eurasia. Hybridisations of this kind might have occurred between Neanderthals and early *Homo sapiens* in Europe and between the *Homo erectus* and early *Homo sapiens* in Southeast Asia. Assimilation model: Smith et al and Trinkaus have argued that the origins of modern human populations was a result of “gene flow” from Africa rather than “human movement”.⁽⁶⁻⁸⁾

Many questions remain unanswered. The time span

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of the domination of *Homo sapiens* varies across the five continents.⁽⁹⁾ Tracing the origins of the anatomically-advanced *Homo sapiens* is a very dynamic activity in modern research. Recently-formulated hypotheses variably support or oppose one or the other of the above-mentioned two conflicting theories. Continuous monitoring and testing of the various hypotheses regarding the emergence of our species is a busy area of research. Knowledge on the origins of the human species requires answers to a range of questions: When? How? Where? To whom? Neither the fossil data nor molecular biological investigations have produced any undisputed agreement among investigating scientists.

WINDS OF CHANGE

Up to the 1960s, multiregional continuity was rarely challenged by physical anthropologists, but this changed with the important work conducted by Howells on human craniometric variation.⁽¹⁰⁾ Howells collected metrical data on 2,504 human crania from 28 ethnic groups representing six major geographical zones, and demonstrated through multivariate analysis that the variation in cranial shape among modern humans is very small. Additional studies by Howells confirmed this conclusion and further demonstrated the lack of any evidence for any continuity between Neanderthals and early European *Homo sapiens*.⁽¹¹⁾ Stringer and Bilsborough also argued that the level of cranial and genetic variation between regional populations of modern humans is very low, and in addition, that the regional differences between recent human populations cannot even be traced back as far as late Pleistocene fossils of *Homo sapiens*.^(12,13) Accordingly, Howells improvised with new multivariate analytical techniques to address the question of how far back in time the craniometric distinctions between recent African, European, East Asian and Australian populations can be traced.⁽¹⁴⁾

He found some cases of late Pleistocene *Homo sapiens* fossils in these different regions, which had their closest relationship with the Holocene inhabitants of the same region, but he also found many cases where this was not true. In addition, when looking at pre-modern fossils (archaic *Homo sapiens*, according to the multiregional continuity theory) anywhere in the world, they had no discernible craniometric relationship with modern humans at all.

Over the last decade, the Out-of-Africa theory has come to be accepted by most researchers, such as Satta and Takahata,⁽¹⁵⁾ Templeton,^(16,17) and Hebsgaard et al.⁽¹⁸⁾ The palaeontological record and calculations based on the “molecular clock” suggest an ancestry for all modern humans of only 200,000 years. The earliest, archaic

members of *Homo sapiens* appear to have spread out all over the world from their origins in South or East Africa. Many researchers no longer regard the Out-of-Africa theory as being in need of further proof, but are instead focusing on the episodes in which modern humans spread from Africa. Lahr and Foley, for instance, have proposed a multiple dispersal model involving a sequence of dispersal events of anatomically-modern *Homo sapiens* both within Africa and also in terms of their routes of migration to Europe and Asia.⁽¹⁹⁾ They partly agreed with the hypothesis of Klein on a “spread and replacement” (based on archaeological evidence) of populations with fully modern behaviour around 40 ka ago, but also recognised that there appear to have been earlier representatives of anatomically-modern *Homo sapiens*, whose behaviour could not be described as being fully modern, outside of Africa in excess of 40,000 years ago.⁽²⁰⁾

CONSCIENTIOUS OBJECTIONS

After the theory of multiregional continuity lost its supremacy in debates on the origins of the anatomically modern *Homo sapiens*, there were still many physical anthropologists who were not prepared to accept the Out-of-Africa theory in its entirety. Our introduction mentioned two intermediate theories between the two main opposing theories, and a third point of view, which attempts to take the middle ground, is Relethford and Harpending’s “weak garden of Eden hypothesis”.⁽²¹⁾ The work of Turner, who proposed Southeast Asia rather than Africa as the geographical centre for the evolution of *Homo sapiens*,⁽²²⁾ should also be noted as an alternative to the two main theories.

Relethford entered the debate with his analysis of Howells’s data on 1,734 human crania from six regions of the world. He concluded that the degree of craniometric variation is very similar to the genetic variation that can be observed from genetic markers and mitochondrial DNA. In all cases, only about 10% of the total variation could be explained in terms of regional differences between populations. According to him, this finding is inconsistent with any theory that assumes a very early origin of an African ancestor, followed by its dispersal into Eurasia and gradual evolution into modern *Homo sapiens* from regional African and Eurasian populations. Any such process would have required unrealistically high rates of continuous gene flow.⁽²³⁾

Relethford accordingly rejected a multiregional model on the origins of modern humans, and accepted that a recent divergence from “a modern population” of African origin was more consistent with his results.⁽²³⁾ Relethford and Harpending expanded on this approach by arguing that

there may have been more than a single factor responsible for the degree of variation between populations within a region.⁽²¹⁾ The range of factors includes the onset time of initial divergence, population size and expansion, and the rates of gene flow and migration. Accordingly, they proposed a model based on within-group morphological variation.

When they analysed the craniometric data for modern human groups from Sub-Saharan Africa, Europe, the Far East and Australasia, they found that the Africans exhibited significantly greater within-group morphological variation than in other parts of the world. One possible explanation could be the later occurrence of a common ancestor for non-African compared to African populations. An early separation of African from non-African populations, followed by the separation between the stem ancestors for European and Asian populations, would explain the results in a manner consistent with the Out-of-Africa or “replacement theory”, as had earlier been argued from the human genetic studies conducted by Cavalli-Sforza et al,⁽²⁴⁾ Cavalli-Sforza,⁽²⁵⁾ and Bowcock et al.^(26,27) On the other hand, an alternative explanation could be found in assuming a greater population size in Africa than the rest of the world; for instance, if Africa’s population over the long term had been approximately three times larger than the size of the non-African population, then the same pattern of within-group morphological variation would be expected to emerge regardless of differences between regional populations in their time depth.

Relethford and Harpending decided that differences between regions in their population size may have been key, a proposition that they labelled the “weak garden of Eden hypothesis”.⁽²¹⁾ Because Africa had contained the majority of the world’s population throughout the Pleistocene, migration and other forms of gene flow had predominantly occurred from Africa to the rest of the world. Thus, populations outside of Africa continually evolved along the same lines as populations within Africa, consistent with the evidence for more affinities than variations comparing African and non-African groups. The evidence for an expansion out of Africa to Eurasia around 100,000 years ago was primarily an expression of this demographical difference. Relethford and Harpending’s hypothesis⁽²¹⁾ could, in addition, accommodate evidence that the Out-of-Africa replacement theory could not, such as the research by Bowcock et al on DNA polymorphisms which suggested that Europeans are a mixture of archaic Asian and archaic African populations. Although non-African genes of African origin constantly flooded populations, they also retained a minority presence of archaic genes of non-African ancestry.^(26,27) Finally, the

larger size of African populations allowed them to harbour greater genetic variation within Africa, compared to other parts of the world, where genetic variation would have been constantly lost through genetic drift.

Turner has proposed that the origins of anatomically-modern *Homo sapiens* are in Southeast Asia rather than Africa, based on dental anthropology.⁽²⁸⁻³⁰⁾ He identified a pattern of dental morphology, which he labelled as Sundadonty. In his early studies, he was particularly concerned with the contrast between Sundadonty and the pattern of dental morphology, which he documented for Northeast Asia and the Americas, and labelled as Sinodonty. He argued that Sundadonty originally dispersed into South China where, over a period of hundreds of millennia, it evolved into the much more complex pattern (involving shovel-shaped incisors, premolar odontomes and other morphological variants) of Sinodonty. Later on, Sinodonty spread into north Siberia and the Americas. Following a similar reasoning, the Japanese scientist Hanihara has suggested that the modification of Sundadonty into Sinodonty was a by-product of adaptation to cold climatic conditions.⁽³¹⁾

Turner then embarked on a survey of populations across the world in terms of their dental morphology. He found that Sundadonty was the least differentiated of all of the world’s dental morphological profiles; in other words, Sundadonty would be the best candidate for being the common ancestor for dental morphology across the world, because this would be the solution that would require the least amount of change from the ancestral to the derived conditions. However, he also recognised that Sundadonty was not identical with the dental morphology of current day Australian and Melanesian populations, even though their ancestry undoubtedly lies in Southeast Asia. Accordingly, Turner recognised a “proto-Sundadont” dental profile to represent the common ancestry between Southeast Asians and Australo-Melanesians. Proto-Sundadonty performed even better than Sundadonty as the hypothesised common ancestor of the dental morphology of modern human populations across the world. Turner did not rule out the possibility that archaic *Homo* populations in parts of the world outside of Southeast Asia may have been incorporated into the expansion of *Homo sapiens* from its Southeast Asian homeland, and in that sense his theory is compatible with multiregional continuity, but his emphasis on a Southeast Asian centre for human evolution makes his position unique among current viewpoints on the topic.

DETAILED STUDIES IN SKULL MORPHOLOGY

Aiello has emphasised that fossil and other cranial evidence in support of the multiregional continuity

theory is concentrated in East Asia and Australasia.⁽³²⁾ She observed that the supporters of multiregional continuity theory see Asia as the ideal testing ground between their theory and the Out-of-Africa theory, given the evidence for the continuity of cranial morphology between the *Homo erectus* in China and the present-day Chinese, as well as that between the *Homo erectus* in Java and present-day Australian Aborigines.⁽³³⁻⁴⁰⁾

Habgood, on the other hand, did not support multiregional continuity notwithstanding his focus on Australasian and Chinese crania. After succeeding in identifying specific facial features in these two regions at the times of *Homo erectus*, Pleistocene *Homo sapiens* and modern *Homo sapiens*, he was unable to trace any line of multiregional continuity.⁽⁴¹⁻⁴³⁾ Other researchers also objected to the approach taken by the multiregional continuity theory supporters, who simply listed “typical” features or characteristic traits of a particular race or a population, and assumed that similar emphases over time demonstrated the transmission of these traits from the chronologically older to the chronologically younger population. These dissenting researchers argued that the recurrence of certain emphases with a high frequency over time may simply be a phenomenon based on size dependency or general “robusticity”. The regional characters touted by supporters of the multiregional continuity theory may simply reflect a retention of primitive characters, which have no value for phylogenetic reconstruction. These researchers include Howells,⁽¹¹⁾ Macintosh and Larnach,⁽⁴⁴⁾ Kaminga and Wright,⁽⁴⁵⁾ and Groves.⁽⁴⁶⁾

As early as 1986, Tattersall declared that there was no direct link between speciation and morphological change, and had noticed that morphological affinities do not necessarily reflect genetic similarities.⁽⁴⁷⁾ Lieberman developed a formal argument in terms of evolutionary systematics.⁽⁴⁸⁾ He argued that any character that is used in authentic tests between the various hypotheses of modern human origins must fulfill three criteria. They must be “developmentally homologous”, meaning that a common character should be the result of shared ancestry rather than convergence; they must be synapomorphic, meaning that they are shared derived characters and not shared primitive retentions; and they must be well-defined and scored consistently during an examination of the relevant modern and fossil specimens of *Homo*, as best illustrated by the work of Lahr.⁽⁴⁹⁾ According to Lieberman, only six of the 33 cranial, mandibular and dental characters that he examined fulfilled all three above-stated requirements.⁽⁴⁸⁾

Of interest in this context is the research into certain apparent “autapomorphies” of the Asian *Homo erectus*. If

also observed in the present-day humans of the Australasian region, these could be recognised as synapomorphies demonstrating some degree of genetic continuity between *Homo erectus* and *Homo sapiens* in the region. Two important salient features of Asian *Homo erectus* include tympanic plate thickness,⁽⁵⁰⁾ and the occurrence of the mastoid fissure and medial recess.⁽⁵¹⁾ None of these studied features show continuity between the Asian *Homo erectus* and recent Australasian populations. This finding falsifies the expectation of supporters of the multiregional continuity theory for a genetic contribution from the Asian *Homo erectus* to present-day *Homo sapiens* in the region.

Robinson carried out an even more detailed study on the human temporal bone.⁽⁵²⁾ She demonstrated that the *Homo erectus* in Asia shows a unique structure to its temporal bone compared to its counterparts, including the *Homo heidelbergensis* in the region of Europe and Africa. On the taxonomic status of the Afro-European *Homo heidelbergensis* and how it differs from its Asian cousin the *Homo erectus*, we suggest referring to the work of Raghavan et al.⁽⁵³⁾ Robinson documented in detail the considerable variations that can be observed on the temporal bone between recent human populations, and identified the distinguishing characteristics of Australian Aborigines. She noted that Aborigines’ long, thick and pointed mastoid process separates them from the other recent populations, but that this is definitely not a feature of the Asian *Homo erectus*. She further observed that the thick tympanic lateral rim of Australian Aborigines would even suggest an affinity with Eskimos. Overall, however, Australian Aborigines show more similarities of the temporal bone with Africans than with populations of other regions, which is consistent with the idea of an African origin for all anatomically-modern *Homo sapiens*, and they do not show any specific similarities with the temporal bone of the Asian *Homo erectus*. Accordingly, she rejected the theory of multiregional continuity outright based on her findings.⁽⁵²⁾

On the other hand, a study by Frayer et al, which included characters from the temporal region, came out in support of multiregional continuity. This study was based on a battery of a dozen features, including mastoid height to width shape. The authors compared this particular feature on the Late Pleistocene Willandra Lakes Hominid (WLH50) from Australia, with its expression on the archaic African *Homo sapiens* from Ngaloba (100-130 ka) and the late *Homo erectus* from Ngandong in Java (around 100 ka). According to them, the 12 features that were compared demonstrated a considerable affinity between the WLH50 and the Ngandong crania, but not with the Ngaloba specimen, contradicting the expectations of the Out-of-Africa theory.⁽⁴⁰⁾

Stringer agreed that the Australasian data on dental and cranial morphology are, when combined, critical for an evaluation of the Out-of-Africa theory.⁽⁵⁴⁻⁵⁶⁾ He, along with many other scientists, recognised the enormous range of variations to be found among the Late Pleistocene (10–30 ka) human fossils of Australia, dating back to the time when New Guinea and Tasmania were still joined to the Australian landmass. However, in his opinion, none of the studies, including those based on the dimensions of the mastoid process and many other non-temporal features, have provided any support for continuity in the Australasian region. He felt that, in spite of the inclusion of the length of the mastoid process in craniometric studies by Howells,^(10,11) Wright,⁽⁵⁷⁾ Kaminga and Wright⁽⁴⁵⁾ and his own study, and the further incorporation of the petrous-tympanic angle along with the suprameatal tegmen, none of the features have provided evidence for continuity between the *Homo erectus* in Java and recent Australian Aborigines. This is one of the main reasons why the above-mentioned investigators have rejected the theory of regional continuity in Australasia.⁽⁵⁴⁻⁵⁶⁾

THE ORIGINS OF MODERN HUMANS: REGIONAL INTERBREEDING AND GENETIC EVIDENCE

The major issue in paleoanthropology seems to be the origins of modern humans, whether from a single regional area, namely Africa, and whether they later replaced the pre-existing archaic humans – the Neanderthals. There are other theories based on human mitochondrial DNA analysis, that humans expanded out of Africa more than once and interbred with the Neanderthals.⁽¹⁶⁾ However, mitochondrial DNA analysis on a clearly dated and one of the latest living Neanderthal remains has shown that the Neanderthal did not contribute to the modern human DNA pool.^(58,59)

The recent partially-mapped Neanderthal DNA studies show that they shared 99.5% of their genetic makeup with modern humans. However, whether they interbred with humans excessively, leading to their extinction, remains questionable.⁽⁶⁰⁾ It should be stressed that the breakdown of DNA during fossilisation as well as the typically soft nature of Neanderthal bones which can easily be contaminated during excavation further complicate the issue. There is also evidence that the archaic morphology of the Neanderthal became more pronounced as they approached the end of the Neanderthal sequence – an idea that is in conflict with the evolutionary anticipation. This indicates that they were not evolving, but rather, degenerating, probably as a result of mutations of some environmental origins.⁽⁶¹⁾

SUMMARY AND CONCLUSIONS

Homo sapiens, the anatomically and intellectually advanced species of the genus *Homo*, evidently originated a long time ago. The supporters of multiregional continuity theory argue that the Asian *Homo erectus* evolved locally into the archaic *Homo sapiens* and then into the anatomically-modern *Homo sapiens*. The morphological changes reflected survival requirements, and “evolution in isolation” might have occurred within the various regions of the world at more or less the same time. The appearance across the Old World of the anatomically-modern *Homo sapiens* between 40 ka and 100 ka, including on the Pleistocene continent of Australia, reflected regional continuity at the subspecies level between middle and late Pleistocene times. According to the Eve, Out-of-Africa or replacement theory, *Homo sapiens* originated in Africa prior to 100 ka, and then dispersed across the Old World to as far away as Australia. This theory is based on interpretations of the skeletal morphological affinities of archaic *Homo sapiens* in Africa, and late Pleistocene *Homo sapiens* outside of Africa, which aligned them with modern humans and distanced these fossils from the Asian *Homo erectus*, which evidently became morphologically more specialised over time.

All the studies agree that certain morphological similarities can be observed between the archaic populations of the *Homo* outside of Africa, and the late Pleistocene fossils assigned to the anatomically-modern *Homo sapiens* within the same region, but there is a sharp difference of opinion in terms of the interpretation of this finding. Supporters of multiregional continuity, such as Brace and Hunt, take this as evidence that modern *Homo sapiens* within this region originated from local ancestry and not from an expansion out of Africa.⁽⁶²⁾ Bilsborough, Lahr, Wood, and Groves, however, dispute this interpretation of the skeletal evidence. They argue that it is most important to remember that the morphological traits used in these comparisons should be non-adaptive (because otherwise the morphological similarities could represent convergent evolution), that they should be shared derived features (synapomorphies) rather than retained ancestral features (or symplesiomorphies), and further that they should be functionally independent rather than mutually dependent.^(13, 63-65)

The continuing debate on the origins of *Homo sapiens* is a result of multiple complexities. Most of the hypotheses, which draw in detail from genetics, human fossils, and the archaeological record, are complex in nature. Very few studies find strong support for multiregional continuity, but not all studies that recognise a major contribution from Africa to the origins of modern humans go as far

as supporting the total replacement of the archaic local populations of the *Homo* species. For example, some studies advocate replacement in one region and some degree of long-term continuity in another. Whether the Asian *Homo erectus* and the European Neanderthals had, in fact, provided any genetic contributions to the later *Homo sapiens* in these regions remains a topic for future research. Multilocus gene studies might yield further insights into human evolution.⁽⁶⁶⁾

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