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978-0-521-12100-2 - Neanderthals and Modern Humans: An Ecological and Evolutionary Perspective
Clive Finlayson
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1 *Human evolution in the Pleistocene*

The origins of humanity may be traced to the tropical African Pliocene, around 6 million years ago (Myr). Genetic evidence has for some time predicted the existence of a common ancestor to chimpanzees and humans around 5–6 Myr (Takahata & Satta, 1997; Gagneux & Varki, 2001). Recent discoveries of African fossils that are claimed to be close to this common ancestor have been dated to between 6 and 7 Myr (Brunet *et al*., 2002).

From this point until the emergence of *Homo erectus* 1.9 Myr ago and its rapid subsequent range expansion (Aguirre & Carbonell, 2001), hominids were confined to sub-Saharan Africa. The estimated number of species that lived during this long period in the Pliocene varies among authors. If we follow a conservative approach (Klein, 1999) we observe a pattern of increasing hominid species richness from about 4.6 Myr with a peak between 1.9 and 1.6 Myr and a sharp decline thereafter (Fig. 1.1). The decline after 2 Myr ago is correlated with increasing climate instability.

The peak in diversity coincides with the first appearance in the fossil record of *H. erectus*. Recently this early African member of the genus *Homo* has been separated from contemporary Asian forms. The name *H. erectus* has been retained for the Asian forms and the name *H. ergaster* for the African (Klein, 1999). Recent evidence suggests, however, that the two significantly overlap in morphology and that they should form part of a geographically diverse species *H. erectus* (Asfaw *et al*., 2002). I follow this latter classification here. Subsequent forms have been given specific status by different authorities although there is considerable uncertainty regarding the precise boundaries of each. The classification of fossils is fraught with difficulties as we shall see in Chapter 4. In this book I consider *H. erectus–H. sapiens* to be a single chronospecies (Cain, 1971) that has repeatedly produced divergent lineages through geographical isolation during the last 1.9 Myr. Some of the described forms are clearly temporal entities within the *H. erectus–H. sapiens* continuum. I include *H. heidelbergensis* and *H. helmei* in this category. Others are divergent lineages that have subsequently become extinct. The Neanderthals are the clearest example of such a divergent lineage and their relationship with mainstream *H. sapiens* will occupy much of this book. Until equivalent fossils are found in Africa it is probably best to regard the form *H. antecessor* from the Spanish site of Atapuerca (Carbonell *et al*., 1995), and possibly also those of Ceprano in Italy (Manzi *et al*., 2001) in this latter category, i.e. a divergent lineage that became extinct.

The question of interbreeding between mainstream *H. sapiens* and divergent lineages when geographical or ecological barriers broke down will be addressed, with specific reference to Neanderthals and contemporary mainstream *H. sapiens*, in Chapter 7. The degree of genetic isolation of the constituent populations would be dependent on a range of factors at any point. These would include distance effects and physical, climatic and ecological barriers. Populations would become isolated at some points and a process of genetic divergence would ensue. Most often such a process would end with renewed contact among populations. At other scales, metapopulations in different regions would become isolated from each other. Gene flow would continue within but not between regions. At even larger spatial scales entire regions would occasionally

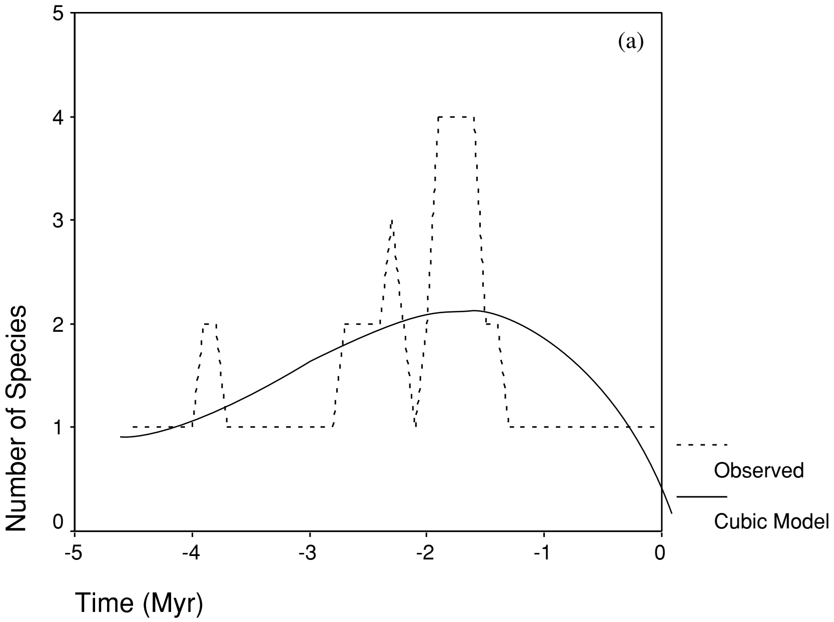

Figure 1.1. (a) Number of hominid species during the last 5 Myr using a conservative number of species. A cubic model best fits the observed pattern: $y = 0.2328 - 2.5022x - 0.9973x^2 - 0.1059x^3$; $R^2 = 0.293$; $P = 0.002$. (b) Decline in hominid species in the last 2 Myr. A cubic model best fits the pattern: $y = 0.8187 - 2.5122x - 5.6201x^2 - 3.1246x^3$; $R^2 = 0.923$; $P < 0.0001$. (c) Relationship between number of hominid species and climate variability (coefficient of variation of temperature) in the last 2 Myr. The pattern is best described by a quadratic model: $y = 10.9797 - 1.9269x + 0.914x^2$; $R^2 = 0.366$; $P = 0.033$.

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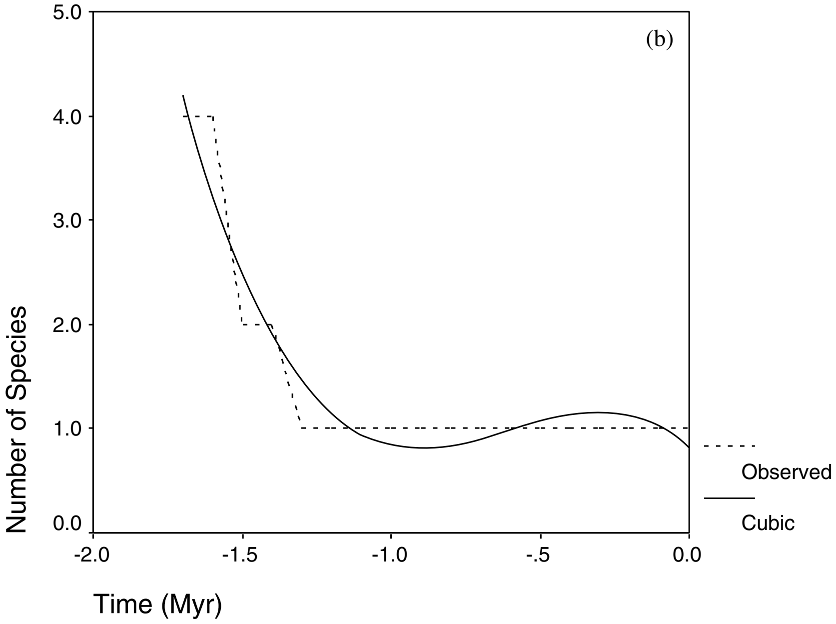

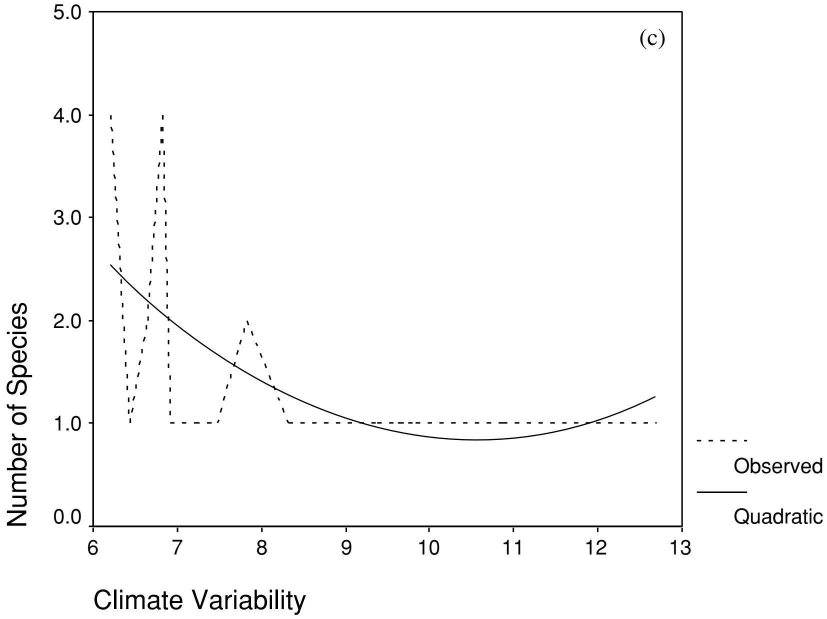

Figure 1.1. (*cont.*)

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become isolated from others. I have introduced scale here and it is an issue that is central to understanding ecology (Levin, 1992) and will appear frequently in this book. In this case we can see how small-scale population isolation events would be expected to be frequent relative to regional events involving many populations.

Populations most distant from each other would be expected to be genetically most distinct but linked to each other by intermediate forms. Where isolation of extreme populations was long, populations at the extremes of the range may have diverged to the extent that they subsequently behaved as good species. In the case of Pleistocene *Homo*, geographical comparisons have to be made among contemporary forms. As we are studying phenomena through time, it is also important that geographical patterns from different time periods are not merged. It is common, for example, to find generalised distribution maps of Neanderthal geographical range in the literature (e.g. Stringer & Gamble, 1993). These should only be regarded as maps of the extremes of the range reached according to currently available evidence. In reality the Neanderthal range, as that of other forms of *Homo* and indeed all other animals, shifted, expanded and contracted through time and it is these range changes that are likely to be most informative about Neanderthal behaviour, as we shall see in Chapter 3 (Fig. 1.2). If we follow this approach, bearing in mind the limitations of the available data, we observe a changing pattern of global distribution of *Homo* in the Pleistocene.

There are two apparently contrasting models that, as we shall see in this book, are in effect extremes of a continuum. Much of the debate that has raged in the last two decades in this respect has been due to differences in the understanding of the evolutionary process and confusion with taxonomic techniques, particularly cladistics. I will start with a brief statement of the two contrasting models.

On the one hand, we have the multiregional model that has been championed by Wolpoff and his school (Wolpoff, 1989). According to this model *H. erectus*–*H. sapiens* is a single species (hence *H. sapiens*). The variations that are observed among fossils simply reflect natural variation as the species has evolved through time. As populations became isolated, so geographical variations arose between them just as they do in most widely distributed organisms. According to this model and its variants, genetic barriers between the populations were never severe enough to cause speciation. Thus present-day human populations reflect a combination of regional variation that dates back to the earliest colonisations and relatively continuous gene flow among the populations. The intensity and frequency of gene flow would be greatest among neighbouring populations and lowest among those geographically most distant.

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Figure 1.2. Maximum limits (grey area) of the Neanderthal geographical range in Europe and western and central Asia. Bioclimate boundaries as in Figure 5.3.

On the other hand, we have the ‘Out-of-Africa 2’ model that has been associated most strongly with Stringer (Stringer & Andrews, 1988). According to this model all natural variation that existed among populations of *Homo* was removed very rapidly after 100 000 years (kyr) ago by the geographical expansion of ‘Modern Humans’ that evolved somewhere in eastern or north-eastern Africa. As these ‘Modern Humans’ spread out of Africa they replaced all existing populations of *Homo* across Africa and Eurasia. These ‘Archaic’ African and Eurasian populations had evolved regionally after an earlier ‘Out-of-Africa 1’ expansion of *H. ergaster* around 1.9–1.8 Myr ago. The model, in its current form, does not negate the possibility of interbreeding among ‘Modern’ and ‘Archaic’ forms on contact but it does assume that no ‘Archaic’ genes persisted into present-day populations.

These ideas may seem very different and irreconcilable but in reality this is not the case. To a large extent the two views reflect a different understanding of the evolutionary process. The multiregional model follows the neo-Darwinian school that sees evolution proceeding through small, cumulative, changes within a species. The macro-evolutionary changes observed in the fossil record are simply the accumulation of many micro-evolutionary changes. Thus *H. ergaster/erectus* gradually evolves into *H. sapiens*. Any division of the lineage into species is of necessity arbitrary. This interpretation is correct. New species arise when populations of a species are isolated from each other sufficiently so that when they secondarily meet they do not hybridise to an extent that the two populations eventually become one (Cain, 1971). Thus the multiregional model, whether correct or not, is consistent with neo-Darwinian evolutionary theory.

In the 1970s and subsequently, Gould & Eldredge (1977) proposed a different evolutionary process. Coming from a palaeontological background these authors had difficulty in understanding how the major steps (such as apparently sudden adaptive radiations) observed in the fossil record could arise through the accumulation of many micro-evolutionary changes. They saw the evolutionary process as a series of major steps punctuated by long periods of stasis during which species shifted their adaptive positions within defined parameters but without significant speciation taking place. No clear mechanism has been satisfactorily defended for such a process. At about the same time a new taxonomic methodology was being developed. Cladistics was seen as a quantitative and objective method of classifying species that significantly improved on existing phylogenetic procedures. By measuring a suite of variables (usually metric), taxonomists were able to separate those that were common to a lineage from those that were specific to a lineage. Whenever such specific differences were observed in a form it was given specific status. Thus, if we understand evolution as being driven by speciation events we move to a situation in which, as new species arise (or are defined cladistically which is not the same thing!), the ancestral ones *de facto* cease to exist. We can now begin to understand why the replacement school (that relies heavily on cladistics) has difficulty in accepting a *H. ergaster/erectus – H. sapiens* continuum. Instead, it sees every new fossil that is discovered and has features specific to its lineage as a new species.

In reality the evolutionary process proceeds in two ways: through the gradual accumulation of small changes within a species and through the formation of new species, in vertebrates at least in geographical isolation, through a process known as allopatric speciation. Recent studies seem to be providing evidence for speciation within a common geographical area through the combination of ecological and behavioural differences within a population (sympatric and parapatric speciation) (Maynard Smith, 1966; Rice & Hostert, 1993; Gavrilets *et al.*, 1998; Dieckmann & Doebeli, 1999; Kondrashov & Kondrashov, 1999; Tregenza & Butlin, 1999; Danley *et al.*, 2000; Filchak *et al.*, 2000; Johannesson, 2001; Porter & Johnson, 2002).

There are inconsistencies in the ‘Out-of-Africa 2’ model that are attributable to not giving importance to gradual micro-evolutionary processes. Thus, if ‘modern humans’ emerged in Africa they must have done so, according to this view, via a speciation event. An alternative, that is more parsimonious and equally valid, is that ‘modern humans’ evolved differences gradually over the last 2 Myr from the ancestor of the hominids that spread to other parts of Africa and into Eurasia. To accept this position would imply acceptance of regional continuity in that part of Africa at least. It is these humans that I term mainstream *H. sapiens*, the ‘Moderns’, in this book.

The next difficulty arises in the definition of species that, as we have seen already, is fraught with difficulties because we are unable to apply the biological species concept to fossils. It is presumably one reason why palaeoanthropologists and archaeologists are so hotly debating the Lagar Velho fossil from Portugal that is purported to be a Neanderthal–Modern hybrid (Duarte *et al*., 1999; Zilhao & Trinkaus, 2002). There is no doubt that the Neanderthals at least were a separate lineage in human evolution. Using cladistics that makes them a separate species. This need not be the case. The Neanderthals may have embarked on a separate evolutionary course from mainstream *H. sapiens* but the degree and time of isolation when the two lineages re-met in the Middle East and later in Europe would have determined whether or not they were a good species. It is largely a question of detail that has little bearing on the study of the two populations other than on the question of interbreeding which will be very hard to resolve in any case. For these reasons I will develop the arguments in this book along the lines of populations as this will be a more productive approach. I will utilise nomenclature only in so far as it aids the reader. Nothing more should be made of the use of particular names.

The multiregional model, on the other hand, does not appear to attach importance to the geographical replacement of one population by another. Yet, there are many examples in the literature of the spread of populations and species, which is a part of the dynamics of the natural world. It seems unlikely that, in the history of the genus *Homo*, there should only have been a single successful ‘Out-of-Africa’ expansion. Implicit in the multiregional model is the failure of any subsequent population expansion other than through genetic assimilation. In the case of the Moderns and the Neanderthals in Europe, it would seem that current evidence clearly indicates the replacement of the Neanderthals by the Moderns. It is a different expectation, and to my mind an unrealistic one, to assume that such replacement need have been worldwide. In any case, as we shall see later, the colonisation of Europe by Moderns need not have been strictly a replacement, if by that we mean an active displacement of Neanderthals by the new arrivals.

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The thrust of this book will, I hope, shed a new light on the processes and the mechanisms that have marked the course of human evolution. The basis of the argument has been marked out by Finlayson *et al*. (2000a) who have adopted a biogeographical approach that sets off from an evolutionary ecology stance. According to this view the growth of Modern Human populations and the decline and extinction of the Neanderthals were independent, climate-linked, events. Modern superiority, leading to the disappearance of the Neanderthals through competition, was considered implausible. The initial colonisation of the world by Moderns was related to a coincidence of climatic and historical events that favoured a population that was adapted to the exploitation of plains mammalian herbivores. The geography of the northern hemisphere and climate-induced vegetation changes coincided to make the colonisation successful.

One of the criticisms of the contrasting models set out above (especially the ‘Out-of-Africa 2’) is that a mechanism has not been put forward to explain the model. Equally, testable predictions have not been generated. In this book I will develop an ecological and evolutionary perspective that attempts to understand human evolution through that of its constituent populations. Climate is seen as a central element that has been critical in human evolution, not necessarily directly as some have postulated (Ruff, 1994; Holliday, 1997a, b) but rather through its effects on the distribution and abundance of plants and animals. I highlight, in particular, the increasing climatic instability during the Pleistocene as a critical factor that has been largely ignored (but see Potts, 1996a, b; 1998), although in my view a new mechanism of ‘variability selection’ is not required, as I will explain later. Running in parallel with the climatic and ecological vicissitudes of the Pleistocene, humans have evolved mechanisms to deal better with these uncertainties. These mechanisms have, in the end, permitted the colonisation of the entire planet.

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2 *Biogeographical patterns*

The distribution and abundance of plants and animals during the Quaternary is of great interest in the understanding of the pattern for any particular species. In our case it is fundamental to understanding the way in which humans were distributed at different times during the Quaternary.

It is important to start our discussion at the macro-ecological scale. The broad biogeographic picture will give us important insights at the scale which is most relevant to our study. We will zoom into lower spatio-temporal scales in later chapters where it is relevant to the discussion. I will not spend time discussing well-established biogeographic patterns that I do not regard to be especially relevant to this book. I am more concerned with the distribution and shifts in distribution of environments that would have influenced human distribution and I will confine my discussion largely to the Eurasian and African land masses which is where the main events took place.

Vegetation structure

In this book I will place particular emphasis on vegetation structure, that is the three-dimensional arrangement of plants in space. The reason for this is that I consider that vegetation structure will have played a major role in the distribution of humans, as it does for most animals (Bell *et al.*, 1991). Vegetation structure would have been particularly important in determining the types of potential prey available to humans and also in making prey visible and accessible. Part of the reason why forests were among the last habitats to be colonised by humans (Gamble, 1993) must have had to do with prey visibility and accessibility as well as density.

We may describe vegetation structure according to the distribution of plants on the ground layer (forbs and grasses), the shrub layer and the tree layer (Kent & Coker, 1992). Even though the species composition will vary significantly between regions of the world, vegetation structure shows similarities. For the purpose of this book I will cluster habitats by vegetation structure into the following blocks.

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Forests

There is a predominance of trees at high density with a dense canopy. Variants include tropical and equatorial rainforests, where the canopy is very high, and temperate broad-leaved forests.

Shrublands

There is a predominance of shrubs with the virtual absence of trees. Today, characteristic examples are the Mediterranean shrublands, known by specific names in different parts of the world (e.g. matorral, chaparral; Cody, 1974).

Open habitats

These are characterised by the absence (or presence in low density as in wooded savannah) of trees and shrubs and a predominance of grasses, forbs, mosses or lichens, or by the total absence of vegetation in patches. Savannahs, steppe and tundra cluster under this definition.

Deserts

Deserts occupy large areas of the planet and are characterised by the virtual absence of vegetation on account of low and irregular rainfall (Cox & Moore, 1985). There are sandy, rocky and ice deserts. Deserts are therefore a separate category of habitat that cannot be described adequately by vegetation structure other than as extreme open habitats. For the purpose of this book I will consider deserts to be a separate category. In human terms deserts have played a major role as barriers to dispersal. Human adaptations to deserts are extreme developments of adaptations to open habitats.

Rocky habitats

These are areas with a minimal vegetation development and a preponderance of a rocky substrate that, like deserts, may be considered extreme cases of open habitats. Unlike deserts they are usually localised at the landscape and regional scales. Two types of rocky habitats have been particularly important to humans. Where the inclination of the land is vertical, or nearly so, rocky habitats are described as cliffs. Cliffs have attracted humans as areas for shelter or where