

## The place of the Neanderthals in hominin phylogeny



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### ABSTRACT

Debate over the taxonomic status of the Neanderthals has been incessant since the initial discovery of the type specimens, with some arguing they should be included within our species (i.e. *Homo sapiens neanderthalensis*) and others believing them to be different enough to constitute their own species (*Homo neanderthalensis*). This synthesis addresses the process of speciation as well as incorporating information on the differences between species and subspecies, and the criteria used for discriminating between the two. It also analyses the evidence for Neanderthal–AMH hybrids, and their relevance to the species debate, before discussing morphological and genetic evidence relevant to the Neanderthal taxonomic debate. The main conclusion is that Neanderthals fulfil all major requirements for species status. The extent of interbreeding between the two populations is still highly debated, and is irrelevant to the issue at hand, as the Biological Species Concept allows for an expected amount of interbreeding between species.

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### Introduction

Neanderthals were given the Linnaean name of *Homo neanderthalensis* after King's (1864) description of the original type-specimens, which he felt were so different from modern *Homo sapiens* that they may even represent a new genus. King's (1864) view contrasts with Huxley's (1863) classification of Neanderthals as a subspecies of human (*Homo sapiens neanderthalensis*), owing to the latter's belief that they could be included in Linnaeus' (1802) *H. sapiens* despite their primitive nature (Tattersall, 2007). The debate continues into modern research, with some believing Neanderthals are sufficiently differentiated to constitute a separate species (e.g. Tattersall, 1986; Holliday, 2006), and others disagreeing (e.g. Dobzhansky, 1944; Currat and Excoffier, 2004). A recent preference for the species classification has arisen (de Vos, 2009), although a group of recent papers using studies of the Neanderthal genome (Green et al., 2010; Mendez et al., 2012; Wall et al., 2013) strongly indicating interbreeding between Anatomically Modern Humans (henceforth AMH) and Neanderthals, has re-awakened the debate.

There is a very real need to return to the rules and methods of traditional taxonomy to further our understanding of what species are and how to identify them. The use of such classification systems is essential for valid conclusions, as they are based on universal patterns found in all species, and thus have to be applicable, despite inherent anthropocentrism and a subsequent belief that

AMH are innately different to other organisms. This article aims to draw from taxonomic biology, identifying the methods of distinguishing species and subspecies *before* assessing the relevant morphological and genetic evidence, as well as the supposed direct evidence of interbreeding between these two populations in the form of hybrids.

### The species 'problem'

The 'species problem' is largely a result of the philosophy and history of the field of taxonomy (Ghiselin, 1974). The main issues can be assigned to three categories: definition and concepts of what constitutes a 'species'; the speciation process; and debates concerning criteria for species identification (Simpson, 1961; de Queiroz, 2005). While species are fundamental to the study of evolution (Tattersall, 1986), they are considered by some to be arbitrary (Dobzhansky, 1935; Foley, 1991), and to lack a single reality over a geographic and temporal range (Simpson, 1951; Foley, 1991; Mallet, 2007).

### Definition of 'species'

The first problem lies in an inconsistency in the use and meaning of the term 'species'. Different definitions include: a rank in a Linnaean hierarchy using individual attributes to encompass all organisms at the species level (Quicke, 1993; Mayr, 1996), the end product of speciation (Nixon and Wheeler, 1990; Shaw, 1998), or the concept of what it is to be a species and what this category

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represents (Kimbel and Rak, 1993; de Queiroz, 1998). Issues arise over the inherent tautology of definitions, with species frequently being defined as ‘whatever a competent taxonomist says is a species’ (Quicke, 1993).

The nature and definition of species is intimately linked to the process of speciation, as species are dynamic parts of this overall process (Harrison, 1998) and can therefore only be an abstract category (Dobzhansky, 1935). Speciation in mammals is a gradual process not an instantaneous event (Simpson, 1951; Mayr and Ashlock, 1991; de Queiroz, 1998), which means we should expect to find organisms representing the entire panoply of stages, not just the end product (Mayr, 1964, 1996; Mayr and Ashlock, 1991). Five such stages have been proposed for gradualistic speciation: local populations, subspecies, semi-species, sibling species, and morphologically different species (Masters, 1993), yet distinguishing between these stages is more difficult.

Species concepts

Most debate is over the true ‘concept’ of species (Hey, 2006), as frameworks for study and identification of species are dependent on the researcher’s species concept (Quintyn, 2009). All concepts are arbitrary to some extent (Reydon, 2004), with different concepts producing different numbers of taxa (Foley, 1991; Balakrishnan, 2005). Some have argued that the ‘Species Concept’ problem is itself a fallacy, as all researchers seem to agree on one concept in the linguistic sense at least, with species being the tip of an evolutionary lineage (Hey, 2006). Fig. 1 gives an indication of the complex development of this area of the philosophy of taxonomy, with the number of current species concepts being at least

23 (Quintyn, 2009). The eight main concepts with relevance to this matter are summarised in Appendix A.

The definitions of species provided by the Phylogenetic and Evolutionary Species Concepts are readily applicable to the Neanderthal species debate, and would support species status in the sense that there is a consistent use of morphology to identify Neanderthal specimens and that this population eventually arrived at extinction. The Recognition Concept (Paterson, 1981) identifies species through species-specific mating recognition systems (SMRS), which have been tentatively inferred in fossil hominins. For instance, as Neanderthals and AMH are clearly different in appearance to palaeoanthropologists, they must at least represent different subspecies (Tattersall, 1992). However this concept has been said to overestimate (Tattersall, 1992) or underestimate (Kimbel, 1991) the number of species, as hominid skeletons do not have obvious morphological features that can be linked to SMRS (Kimbel, 1991), and its tautological nature has been revealed upon application to extant primates (Jolly, 1993).

Most debate over species classification uses the Biological Species Concept proposed by Mayr (1964) and Dobzhansky (1935), which defines species as reproductively isolated populations. According to the criterion of complete reproductive isolation, Neanderthals and AMH would have to be classified as the same species if interbreeding did occur. Yet this strict criterion was objected to by both Darwin and Wallace. Wallace took his objection further by highlighting the circular reasoning of defining and delimiting a taxon by the same criteria (Mallet, 1995). The requirement of complete reproductive isolation is a common misconception: Mayr himself acknowledged that occasional hybridisation occurs between sympatric species (Mayr, 1964, 1996), as isolation mechanisms do not prevent all interbreeding, with their main role

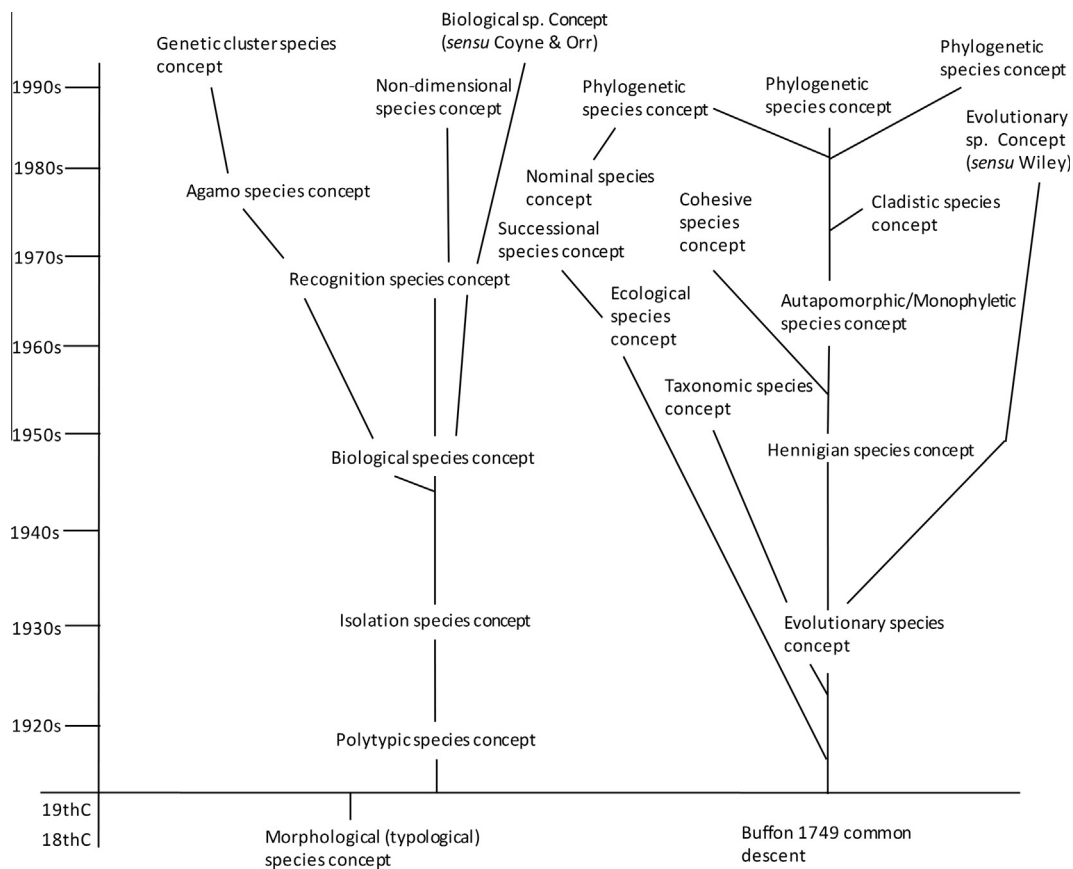


Fig. 1. ‘Phylogeny’ of species concepts (Quintyn, 2009: 310).

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