ANTHROPOLOGIE • XLIII/2–3 • pp. 207–213 • 2005

IAN TATTERSALL

SPECIES CONCEPTS AND HOMINID DIVERSITY IN LATER PLEISTOCENE EUROPE

ABSTRACT: The concept of the species continues to elude easy definition, and indeed it seems true that different contexts will always demand different definitions. Morphology must necessarily be the principal criterion for species recognition in the fossil record, and Jolly's (2001) recent perception that morphologically differentiated African baboon populations may simultaneously serve the roles of "biological" subspecies and "phylogenetic" species places us in a better theoretical position to infer that adequately distinctive fossil morphs do indeed represent the historically individuated entities which conventionally warrant recognition as species. In this article I briefly examine how different notions of the species and their role in evolutionary process have affected the perception of pattern in the hominid fossil record, and point out that on the basis of unusually rich fossil documentation the species Homo neanderthalensis *emerges as an entity that in evolutionary terms was entirely distinct from* Homo sapiens. *Further, it appears that this species formed part of a larger endemic European clade that, in the form of the hominid found at the Sima de los Huesos, coexisted with* Homo heidelbergensis *as represented by the Mauer and Arago hominids. Evidently, hominid evolution in Europe, prior to the relatively recent incursion of* Homo sapiens*, was not limited to the progressive evolution of a single endemic lineage.*

KEY WORDS: Species concepts – Homo neanderthalensis – Homo sapiens *– Neanderthals – Hominid fossil record – Evolutionary entities – Paleoanthropology*

INTRODUCTION

The sheer luxuriant diversity of Jan Jelínek's intellectual interests makes it easy to find a subject appropriate for the celebration of his memory, but at the same time difficult to know quite where to start. However, given that every one of Jan's practical paleoanthropological concerns was underpinned by his acute awareness of the importance of underlying process, it would seem legitimate in this memorial volume to address briefly the notion of the species as both a biological and a systematic entity, and to consider how variations in the way this fundamental unit is conceived have affected the ways in which the hard evidence of the hominid fossil record has been interpreted over Jan Jelínek's professional lifetime, particularly in his home ground of Europe.

NOTIONS OF THE SPECIES

As long ago as 1865 Pierre Trémaux wrote that "of definitions of species, there are as many as there are naturalists," and the situation has not materially changed in the century and a half since (Trémaux 1865:133–134). Indeed, the number of species definitions on offer has swelled by dozens in the last few decades alone (Hey 2001), and there appears to be little immediate prospect of anything approaching a consensus on this matter. During the first half of the twentieth century the great contribution of the Evolutionary Synthesis to this debate was to eliminate older typological notions of the species (e.g. Dobzhansky 1937) and to emphasize the importance of population isolation in the emergence of new vertebrate species (e.g. Mayr 1942). Still, under the umbrella of the Synthesis the idea that species consist of genetically dynamic populations whose members resemble each other because they belong to the same species rather than vice versa, was still able to coexist with the omnipresent if usually implicit belief that species were somehow not "real" entities. For although the Synthesis insisted on the importance of isolating mechanisms for keeping nature divided into self-contained units at any one point in time (the "biological species concept"), especially in its later "hardened" versions it preached an essentially transformationist vision of the evolutionary process (see Mayr 1963). In practice, the proposition became that Darwin's nuanced idea of "descent with modification" boiled down to little more than the gradual generation-by-generation genetic and phenotypic modification of reproductively isolated lineages under the guiding hand of natural selection. In evolutionary time, then, species became seen as essentially ephemeral segments of steadily transforming lineages. Lacking natural boundaries in time, they could in this dimension only be defined arbitrarily – which ironically made the famous and otherwise regrettable "gaps" in the fossil record into paleontological conveniences.

With the emergence of the notion of punctuated equilibria (Eldredge, Gould 1972) an awareness began to dawn that the evolutionary process is a great deal more multifactorial than the seductive reductionisms of the hardened Synthesis admit; and the relevance of this realization to notions of the species was thrown into focus by Ghiselin's (1974) proposal that species are *individuals*, rather than categories or classes. In the new perspective created by these insights, species became bounded historical as well as ecological/reproductive entities, with least potentially identifiable births (at speciation), lifespans (histories) and deaths (at extinction). And this in turn forced paleontologists to come to terms with the fact that a fossil's age could no longer be considered an infallible criterion for understanding its place in an evolutionary schema. For those schemas could no longer be seen as invariably linear; instead, evolving lineages often show complex branching patterns in which not only do the various actors (species) need to be identified, but their relationships analysed, on grounds other than time.

In the majority of recent neontological approaches to defining the species, the basic unit into which nature is "packaged," reproductive boundaries have been seen as the key, whether the definitions involved have been "exclusive" (focussing on the barriers that impede reproduction *between* members of differentiated populations) or "inclusive" (emphasizing factors that contribute to reproductive cohesion *within* populations). But under any approach whatever, in its application the criterion of reproduction often leaves a vast gray area where very close relatives are concerned. For in the vast majority of such instances our evidence is likely to be behavioural, and individual behaviours do not necessarily provide a touchstone for effective genetic separation. It is clear, for example, that the reproductive behaviours often observed among captive members of related groups do not provide convincing evidence that they belong to the same species, even where apparently viable zygotes are produced. Indeed, even the existence of documented hybrid zones in nature is no guarantee of the historical individuation of the two populations concerned unless progressive and continuing introgression of the two gene pools can be shown to be occurring – something that could potentially take centuries to demonstrate among long-lived organisms such as primates. So while the lack of observed instances of coupling among members of two differentiated groups that are in some form of contact can be taken as prima facie evidence of species separation, observations of the reverse situation still potentially leave a yawning area of uncertainty.

For the paleontologist the matter of "reproductive compatibility" is, of course, entirely an inferential matter. For systematic purposes, only three lines of evidence are available to those studying fossils: morphology, age, and geographical locality. Since neither age nor locality has any *necessary* relationship to systematic position (Eldredge, Tattersall 1975), the principal focus of the paleontologist has to be on morphology. But even here the difficulties are legion. Local populations of any widespread vertebrate species typically tend to differentiate morphologically, and such differentiation appears to be entirely independent of speciation, the process that gives rise to new species (Tattersall 1994). But to put the matter in precisely these terms is probably misleading, for speciation itself is almost certainly not a unitary mechanism. Instead, speciation is a *result*, one that we observe *a posteriori*, and that, very significantly, may eventuate from molecular developmental changes of many different kinds. What speciation is certainly *not*, however, is simply a passive sequel to accumulating morphological change. Very high levels of morphological differentiation can accumulate among local populations that nonetheless remain firmly within the same species, while speciation can apparently have occurred among closely related local populations that differ to the eye little if at all. Evidently, there must in principle be a limit to which local populations within a species can differentiate morphologically before speciation intervenes; but in practice that limit is poorly defined and highly variable.

This is, of course, why it is necessary to be wary of the attractions of the "phylogenetic species concept" (PSC) that has lately been gaining in popularity among neontological systematists as well as paleontologists. This concept regards the phylogenetic species as "the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent" (Cracraft 1983: 170). The emphasis here is on (morphological and, latterly, genetic) diagnosability, and the PSC deliberately omits reproductive disjunction from other species-level entities as a criterion for species status, emphasizing within-population reproductive cohesion instead. But even this nod to reproduction is essentially *pro forma*, and in practice the essential element of the PSC normally resides in the morphological distinctiveness of the species units it recognizes. The attractions of this notion to the morphology-bound paleontologist are evident, and Cracraft is certainly correct to argue that in practice all evolutionary units have to be diagnosable. However, it sadly remains true that not all diagnosable units will be historically individuated from their closest relatives. If speciation is independent of morphological shift, then the morphological novelties that create diagnosable units will often be present in the ancestral subspecies that has differentiated *before* speciation (i.e. historical individuation) occurs. Apomorphies of like kind may, however, also be acquired later, in the round of geographical/morphological differentiation that, in any successful widespread population, will precede the next speciation event in the sequence. In which case, of course, a reproductively cohesive unit might conceivably be differently diagnosable morphologically at different times in its existence. And an effectively similar result might equally come about by loss of distinctive characters through hybridisation.

Clearly the complexities of population movement and dynamics, as well as the simultaneous operation of unrelated evolutionary processes, ensure that the effort to diagnose discrete fossil and even living populations at the lowest taxonomic levels will always be fraught with some degree of uncertainty. Indeed, on the basis of his and colleagues' extensive observations of natural hybridisation among parapatric and morphologically differentiated populations of baboons in various parts of Africa, Clifford Jolly (2001: 177) has been moved to speculate that baboon allotaxa may simultaneously be "'phylogenetic' species, but 'biological' subspecies." He further suggests that the pattern observed in these cercopiths might be considered as a model for hominid evolution, particularly its early stages. Together with the considerations outlined above, propositions such as Jolly's negate the practical value of agonizing too precisely over what species intrinsically are. Uncomfortable as our intuitively reductionist minds might find propositions such as these, it seems at the very least evident that although Nature is unquestionably packaged, it is incurably untidily packaged, and at the finest levels of morphological/systematic differentiation it presents us with a framework of uncertainty within which we shall simply have to learn to live. The lesson for the paleontologist is surely to proceed conservatively when making species distinctions in the fossil record, and to err (though not overzealously: see below) on the side of inclusivity. For even if such a procedure may miss subtle phylogenetic events, it will not distort the overall evolutionary pattern as excessive fractionation might.

INTERPRETATION OF THE HOMINID FOSSIL RECORD

Probably the most influential theoretical contribution to paleoanthropology of the entire twentieth century was penned by the ornithologist Ernst Mayr in 1950. In that classic symposium paper this giant of the Synthesis decried the lavish splitting tendencies of paleoanthropologists over the first half of the century – tendencies that had unarguably led to an unnecessarily complicated and chaotic nomenclature of fossil hominids. Claiming that a greater variety of morphologies existed within the (highly speciose) single insect genus *Drosophila* than within the entire then known "suborder Anthropoidea", Mayr proposed placing all fossil and living hominids within the single genus *Homo*, with a temporal succession of species leading from *H. transvaalensis* (the australopiths) through *Homo erectus* to *Homo sapiens* (in which he included the Neanderthals). And he did this on the explicit assumption, entirely in line with the dogma of the hardened Synthesis that had by then emerged, that "never more than one species of man existed on the earth at any one time" (Mayr 1950: 116). The capitulation of paleoanthropology to this new perspective was almost instantaneous, and largely complete. And it is certainly true that in sweeping away a huge accumulation of largely unsorted intellectual debris the outsider Mayr had performed a huge service to the paleoanthropological profession, not least by providing a novel mindset for a new post-war generation of paleoanthropologists, prominent among them Jan Jelínek, who were already dissatisfied with the rather mindless and unstructured proliferation of names that had been bequeathed them by their predecessors.

Frequently, oversimplification is required before a proper appreciation of complexity can be achieved, and this was certainly the case in paleoanthropology as the twentieth century passed its midpoint and an era of increasingly intense fossil discovery began. As far as the European hominid fossil record was concerned, Mayr's attack on the status quo rapidly entrenched the notion that this record contained evidence of only two hominid species: *Homo erectus* and *Homo sapiens* (see review by Tattersall 1995a). Indeed, Mayr's structures seem to have frightened some authorities off Linnean nomenclature altogether. For example, in the early 1950s, with the fraudulent Piltdown and misdated Galley Hill fossils eliminated from consideration, Clark Howell (1951, 1952) was able to envisage a single lineage in Europe that led from Mauer through Swanscome to Steinheim and thence to an "early Neanderthal" assemblage containing such forms as Saccopastore 1 and Ehringsdorf. At the same time he also perceived a geographical trend, with western European early Neanderthals culminating in the "classic" Neanderthals of the Last Glacial and their eastern counterparts trending toward more modern-appearing Mount Carmel-like populations. Howell was, however, sufficiently impressed by the evidence for abrupt replacement of the western European classic Neanderthals by modern people to reject the notion of intermixing between at least classic Neanderthals and moderns. Still, perhaps somewhat in shock from Mayr's radical proposal, nowhere in his long papers did Howell give a Linnean name to any of the forms he mentioned – a practice to which he continued to adhere for decades.

Jan Jelínek, on the other hand (e.g. Jelínek 1969), was more systematically explicit. Based largely on his important early studies of the Brno and other Moravian hominid fossils (e.g. Jelínek 1951, 1957) he saw substantial morphological (and technological) within-site as well as between-site variation among late Pleistocene hominids of central and eastern Europe, but insisted nonetheless on distinguishing Neanderthals and moderns at the subspecies level, as *Homo sapiens neanderthalensis* and *Homo sapiens sapiens*, respectively. Other authors also used infraspecific nomenclatural devices to express perceived variety in the later Pleistocene European record; Thoma (1966), for example, applied the rather fanciful name *Homo (erectus* seu *sapiens) hungaricus* to the Vérteszöllös fossil, in order to express his view that it was "transitional" between *Homo erectus* and *H. sapiens*. In the spirit of the Synthesis, Jelínek himself (e.g. 1986) later forcefully made the case for including the "anteneanderthals" in *Homo erectus*, and indeed went so far as to suggest including that species, with its many variants, within *Homo sapiens.*

In recent years several factors have affected the interpretation of the European fossil record. Three are of particular importance. One of these is the emerging recognition that *Homo erectus* is best regarded as an endemic and terminal Eastern Asian species, with no direct relevance to hominid phylogeny in Europe (see Schwartz, Tattersall 2000, Tattersall, Schwartz 2000). Another is the realization that the Neanderthals are much more distinctive morphologically than could justify their absorption into *Homo sapiens* (Tattersall 1986). And the third and most important is the huge accretions to the record that have been made in recent decades. These additions have led just in the past few years to the naming of at least two distinctive new European hominid species from the terminal lower Pleistocene: *Homo antecessor* (Bermudez de Castro *et al.* 1997) and *Homo cepranensis* (Mallegni *et al*. 2003). As discussed below, the story of hominid evolution in Europe has been a much more complex, and much less unilinear, matter than Mayr and his immediate successors had imagined. But there is nonetheless a strong argument to be made that the outlines of that more complex story would still not be properly discernible without the essential housecleaning that was carried out in the 1950s and 1960s by Jelínek, Howell and other members of what might be called "the Synthesis generation." The remainder of this contribution looks briefly at the emerging shape of hominid phylogeny in Europe during the later part of the Pleistocene.

THE HOMINID FOSSIL RECORD IN MID-LATE PLEISTOCENE EUROPE

As the discussion at the beginning of this essay suggests, recognizing historically individuated units in the fossil record of any group of organisms is not easy. And perhaps it is harder in our family Hominidae than in most, since the sheer morphological diversity of the hominid record, especially over the last two million years (myr) or so, is indicative of a very eventful history. For in comparison with most mammal groups the turnover of morphologies (and by extension presumably of species) has apparently been unusually rapid among the hominids. Given the difficulty of equating any particular quantifiable level of morphological shift to speciation, it seems most prudent to be conservative in awarding species status to morphologically distinctive aggregations of fossils, and to recognize as separate species only those groups of fossils that are not only very strongly characterized morphologically but that show a significant amount of temporal persistence in the fossil record.

Particularly notable in this regard are the Neanderthals. For these hominids are characterized not only by a whole suite of apomorphies of the cranial and postcranial skeletons (see Tattersall 1995b, Tattersall, Schwartz 2000), but they are known as an easily identifiable entity from a large number of sites dating from before the beginning of the late Pleistocene almost to its end. There is by now, indeed, no assemblage of hominid fossils that more clearly warrants recognition as a historically individuated species than does that composing *Homo neanderthalensis*, and there has been remarkably little disagreement over which fossils are properly classifiable as Neanderthals. Cranial apomorphies of this species, as listed by Schwartz and Tattersall (2005) and Tattersall and Schwartz (in press), include: double-arched supraorbital ridges whose surfaces roll smoothly upward from the orbital roofs and onto the frontal squama; orbits that are obliquely truncated inferomedially; a narrow lower face and a sharply retreating midface; medial projections emerging above a spinoturbinal crest that delineates a prenasal fossa lying just within the very large nasal aperture; very long and typically thin zygomatic arches; a "puffy" midface that reflects the presence internally of expanded maxillary sinuses that swell out the infraorbital and medial orbital regions; an angulation along the anterior squamosal suture, delineating distinct anterior and posterior temporal fossae; a smoothly rounded ("en bombe") cranial profile in rear view; a pitted suprainiac fossa that lies above a superior nuchal line that is undercut by the nuchal plane but poorly delineated above; a long and more or less straight parietomastoid suture that flows directly behind into an anterior lambdoid suture; widespread pneumatisation within the petrosal; incomplete ossification of the ectotympanic tube laterally; and a long, narrow, ovoid foramen magnum. In the mandible are seen retromolar spaces; sigmoid notches that are deepest posteriorly, in front of low-set condyles, and sigmoid notch crests that terminate medial to the lateral extremities of the condyles; obliquely truncated gonial angles; symphyseal bone that, when seen from below, is thinner buccolingually than the bone distal to it. In the dentition the molars have relatively complex occlusal surfaces, with centroconids and centrocones present on the lower and upper molars respectively, and distinct talonid and trigonid basins in the relatively long and narrow lowers. The molar occlusal

FIGURE 1. Comparison of the Sawyer/Maley reconstructed Neanderthal skeleton (left) with a modern *Homo sapiens* individual of similar stature. Photo courtesy of Ken Mowbray.

surfaces are well defined peripherally by blunt crests, and are constricted in area by their inwardly sloping sides.

This list of apomorphies is as generous as that available for any widely recognized extinct hominid species, and even though (unremarkably) not all Neanderthals show all of these features with equal strength of expression, and some of these characteristics may occasionally be matched elsewhere among the hominids, this is only to be expected in a phylogenetically close-knit group such as the genus *Homo*. All species populations are morphologically and otherwise variable, and the occasional bulging occipital in an early *Homo sapiens*, or restrained supraorbital development in an adult Neanderthal, provide no justification for claims of "intermediacy".

In the event that there should be any doubts about this, a reconstruction of an entire Neanderthal skeleton recently completed at the American Museum of Natural History (Sawyer, Maley 2005) should help allay them. This reconstructed skeleton, assembled from parts of five incomplete Neanderthals but demonstrably reliable in its body proportions because of comprehensive representation from the La Ferrassie 1 Neanderthal individual, is compared to a *Homo sapiens* skeleton of similar stature in *Figure 1*. Prior to this reconstruction it was well known that Neanderthals differed from modern humans in numerous significant details of the body skeleton as well as of the cranium: features such as the expansive joint articular surfaces, the thick-walled long bones, and the flaring pelvis with its broad ilia and long, slender pubic rami have long been remarked. But the enormous *Gestalt* differences between *Homo neanderthalensis* and *Homo sapiens* only become fully evident when the two assembled skeletons are seen side-by-side. In particular, the (probably primitive) shape of the Neanderthal thorax contrasts strongly with that of modern humans, which tapers both at the top and the bottom. The Neanderthal rib cage is narrow at the top and flares greatly towards its bottom edge, to match the very wide pelvis. The junction of the latter with the vertebral column is also set lower in the pelvic bowl, contributing to an extreme shortness of the waist that would, by limiting torsion of the trunk, have significantly affected gait as well as outward appearance. Clearly, *Homo neanderthalensis* and early *Homo sapiens* would have presented very different figures on the ancient landscape, adding to the highly suggestive morphological evidence for species separation, a strong basis for the inference that hominids of the two kinds would have possessed very different specific mate recognition systems, a significant element under "exclusive" and "inclusive" species concepts alike.

Once it has been established that in the late Pleistocene of Europe and western Asia there existed an endemic hominid species that, as attested both by morphological (Tattersall, Schwartz 2000) and molecular information (Krings *et al.* 1997), possessed both a long separate evolutionary history and no obvious close relationships to coeval hominids from other areas of the world, we can begin to ask where within the hominid family this form, *Homo neanderthalensis*, fits. And particularly with the improved fossil record of the last few decades to hand, it immediately becomes clear that the features traditionally associated with *Homo neanderthalensis* are not confined to that species. In the European later Pleistocene record there exist fossils and fossil assemblages that share some of the Neanderthal apomorphies, but not all of them. Prominent among such fossils is the probably around 225 kyr-old Steinheim cranium, which possesses a very Neanderthal-like morphology of the upper face and various other areas of the skull (see Schwartz, Tattersall 2005), but departs from the Neanderthal condition in the midface and cranial profiles and as a result has never been identified as a Neanderthal. Schwartz and Tattersall (2005) have suggested that, in consequence, Steinheim is best viewed as representing a sister taxon to *Homo neanderthalensis*. Similarly, the large and fairly homogeneous hominid assemblage from the Sima de los Huesos at Atapuerca, probably about 400 kyr old (Bischoff *et al.* 2003) shares a less extensive suite of cranial apomorphies with both Neanderthals and Steinheim but is cranially distinct from both and most plausibly represents a sister to the Neanderthal-plus-Steinheim clade.

If the wider clade containing the Neanderthals was thus established in Europe by around 400 kyr ago, it becomes clear that the picture of hominid evolution in Europe was not a strictly linear one. For coeval with the Sima hominids is *Homo heidelbergensis* (based on the Mauer jaw that is in turn directly comparable to the Arago hominid assemblage; this latter includes substantial cranial elements which evoke comparisons with the Greek Petralona cranium). Both the Arago 21 face and the more or less complete Petralona cranium show a morphology of the upper face that is extremely non-Neanderthal like, with very tall supraorbital surfaces that peak around mid-orbit and that twist anterosuperiorly in front of d distinct edge demarcating the shallow posttoral sulcus behind. These features, and others, unite European *Homo heidelbergensis* with a cosmopolitan group of fossils from sites in Africa and eastern Asia, and distinguish it from the apparently endemic European Neanderthal clade. Evidently, more than one kind of hominid was resident in Europe in the later part of the middle Pleistocene, and if we factor in fossils such as those from Bilzingsleben (Schwartz, Tattersall 2005) the picture may ultimately turn out to be more complex yet.

CONCLUSION

Although it is true that diagnosability does not by itself guarantee historical individuation, a general survey of variation within speciose primate genera suggests that it is vanishingly improbable that morphological differences on the scale that distinguish Neanderthals from modern humans could usefully be accommodated within a single biological species. Indeed, if Jolly (1991) is correct in speculating that "biological" subspecies may in certain cases equate with "phylogenetic" species, it is probably safe in a phylogenetic sense to regard the morphologically differentiated and easily diagnosable taxa represented by the Steinheim, Sima and Mauer fossils as historically individuated units irrespective of their unknowable "biological" status, and thus as individual actors in the human evolutionary play. It is now becoming evident that on the systematic level the plot of this play was a lot more complex than was envisaged (on the basis of a much smaller fossil record than is now available) by Jan Jelínek and the other paleoanthropologists of the "Synthesis generation." But scientific knowledge is by its nature always provisional; and the patterns we currently perceive could never have begun to emerge without the essential labours of those gifted scientists. As ever, we are standing on the shoulders of giants.

ACKNOWLEDGMENTS

I thank Dr. Marta Dočkalová and the staff of Anthropologie for this opportunity to honour the memory of our greatly lamented friend and colleague Jan Jelínek, and Jeffrey Schwartz for years of discussion of the matters reviewed here.

REFERENCES

BERMUDEZ DE CASTRO J. M., ARSUAGA J.-L., CARBONELL E., ROSAS, A., MARTINEZ I., MOSQUERA M., 1997: A hominid from the lower Pleistocene of Atapuerca: Possible ancestors to Neandertals and modern humans. *Science* 276: 1392–1395.

BISCHOFF J. L., SHAMP D. D., ARAMBURU A., ARSUAGA J. L., CARBONELL E., BERMUDEZ DE CASTRO J. M., 2003: The Sima de los Huesos hominids date to beyond U/Th Equilibrium (>350 kyr) and perhaps to 400–500 kyr: New radiometric dates. *J. of Archaeological Science* 30: 275–280.

CRACRAFT J., 1983: Species concepts and speciation analysis. *Curr. Ornithol.* 1: 159–187.

DOBZHANSKY T., 1937: *Genetics and the Origin of Species*. Columbia University Press, New York. 364 pp.

ELDREDGE N., GOULD S. J., 1972: Punctuated equilibria: An alternative to phyletic gradualism. In: T. J. M. Schopf (Ed.): *Models in Paleobiology*. Pp. 82–115. Freeman, Cooper Co., San Francisco.

ELDREDGE N., TATTERSALL I., 1975: Evolutionary models, phylogenetic reconstruction, and another look at hominid phylogeny. In: F. S. Szalay (Ed.): *Approaches to Primate Paleobiology.* Pp. 218–243. S. Karger, Basel.

GHISELIN M. T., 1974: A radical solution to the species problem. *Syst. Zool.* 23: 536–544.

HEY J., 2001: *Genes, Categories and Species*. Oxford University Press, New York. 217 pp.

HOWELL F. C., 1951: The place of Neanderthal man in human evolution. *Amer. J. of Phys. Anthrop.* 9: 379–416.

HOWELL F. C., 1952: Pleistocene glacial ecology and the evolution of "Classic Neanderthal" man. *Southwest J. of Anthrop.* 8: 377–410.

JELÍNEK J., 1951: A contribution to the classification of the Moravian (Czechoslovakia) Upper Palaeolithic man. *Acta Musei Moraviae* 36: 55–64.

JELÍNEK J., 1957: La nouvelle datation de la découverte de l'Homme fossile Brno II. *L'Anthropologie* 61: 513–515.

JELÍNEK J., 1969: Neanderthal man and *Homo sapiens* in Central and Eastern Europe. *Curr. Anthrop.* 10: 475–503.

JELÍNEK J., 1986: Position des anténéanderthaliens parmi les hominidés. *L'Anthropologie (Paris)* 90: 495–501.

JOLLY C. J., 2001: A proper study for mankind: Analogies from Papionin monkeys and their implications for human evolution. *Yearbook of Phys. Anthrop*. 44: 177–204.

KRINGS M., STONE A., SCHMITZ R. W., KRAINITZKI H., PÄÄBO S., 1997: Neandertal DNA sequences and the origin of modern humans. *Cell* 90: 19–30.

MALLEGNI F., CARNIERI E., BISCONTI M., TARTARELLI G., RICCI S., BIDITTU I., SEGRE A., 2003: *Homo cepranensis* sp. nov. and the evolution of African-European Middle Pleistocene hominids. *C. R. Paléovol*. 2: 153–159.

MAYR E., 1942: *Systematics and the Origin of Species*. Columbia University Press, New York. 334 pp.

MAYR E., 1950: Taxonomic categories in fossil hominids. *Cold Spring Harbor Symp. Quant. Biol.* 15: 109–118.

MAYR E., 1963: *Animal Species and Evolution*. Harvard University Press, Cambridge MA. 797 pp.

SCHWARTZ J. H., TATTERSALL I., 2000: What constitutes *Homo erectus*? *Acta Anthrop. Sinica* 19 (Suppl.: Proc. 1999 Beijing International Symposium on Paleoanthrop.): 18–22.

SAWYER G. J., MALEY, B., 2005: Neanderthal reconstructed. *Anat. Rec. (New Anat.)* 283B: 23–31.

SCHWARTZ J. H., TATTERSALL I., 2005: *The Hominid Fossil Record, vol. 4*. Wiley Liss, New York. 551 pp.

TATTERSALL I., 1986: Species recognition in human paleontology. *J. of Hum. Evol.* 15: 165–175.

TATTERSALL I., 1994: How does evolution work? *Evol. Anthrop.* 3, 1: 2–3.

TATTERSALL I., 1995a: *The Fossil Trail: How We Know what We Think We Know about Human Evolution.* Oxford University Press, New York. 276 pp.

TATTERSALL I., 1995b: *The Last Neanderthal: The Rise, Success, and Mysterious Extinction of Our Closest Human Relatives.* New York, Macmillan. 208 pp.

TATTERSALL I, SCHWARTZ J. H., 2000: *Extinct Humans*. Westview Press, Boulder CO. 256 pp.

TATTERSALL I., SCHWARTZ J. H., *in press*: The distinctiveness and wider systematic context of *Homo neanderthalensis*. In: K. Harvati, T. Harrison (Eds.): *Neanderthals Revisited: New Approaches and Perspectives*. Springer, Berlin.

THOMA A., 1966: L'occipital de l'Homme mindélien de Vérteszöllös. *L'Anthropologie* 70: 495–534.

TRÉMAUX P., 1865: *Origine et transformations de l'homme et des autres êtres*. Hachette, Paris. 248 pp.

Ian Tattersall
Division of Anthropology
American Museum of Natural History
Central Park West at 79th Street
New York, NY 10024, USA
E-mail: iant@amnh.org