

Morphology, Paleoanthropology, and Neanderthals

IAN TATTERSALL AND JEFFREY H. SCHWARTZ

Morphology carries the primary signal of events in the evolutionary history of any group of organisms but has been relatively neglected by paleoanthropologists, those who study the history of the human species. Partly this is the result of historical influences, but it is also due to a rather fundamentalist adherence among paleoanthropologists to the tenets of the Neodarwinian Evolutionary Synthesis. The result has been a general paleoanthropological desire to project the species *Homo sapiens* back into the past as far and in as linear a manner as possible. However, it is clear that the human fossil record, like that of most other taxa, reveals a consistent pattern of systematic diversity—a diversity totally unreflected in the conventional minimalist interpretation of that record. Thus, the Neanderthals, both morphologically and behaviorally as distinctive a group of hominids as ever existed, are conventionally classified simply as a subspecies of our own species *Homo sapiens*—a classification that robs these extinct relatives of their evolutionary individuality. Only when we recognize the Neanderthals as a historically distinctive evolutionary entity, demanding understanding in its own terms, will we be able to do them proper justice. And we will only be able to do this by restoring morphology to its proper place of primacy in human evolutionary studies. *Anat. Rec. (New Anat.)* 253:113–117, 1998. © 1998 Wiley-Liss, Inc.

KEY WORDS: human evolution; morphology; systematics; species; Neanderthals

Morphology is the very keystone of studies of the fossil record, for, in dramatic contrast to both time and geography, the other basic attributes of the ancient teeth and bones that make up this record, it is morphology alone that bears the clear imprint of evolutionary history.¹ Spatial distribution is affected by a wide variety of

adventitious influences, and the temporal ranges of fossil taxa are invariably incompletely known; but, at some level of resolution, morphology invariably carries the signal of phylogenetic relationship. Yet it takes no more than a glance at the history and current practice of paleoanthropology to indicate that morphology has never occupied the central place it merits in the science of human origins.²

This deficit is due at least in part to historical accident. Unlike other fields of vertebrate paleontology, which originated in the study of comparative anatomy and whose practitioners are necessarily interested in the origins of diversity in groups of organisms, human paleontology was founded by students of human anatomy. The work of these scientists and their intellectual descendants has combined an exquisite sensitivity to within-species variation with a desire to project the single species *Homo sapiens* as far back into the past as the record permits—and preferably in the most linear manner possible. Today this tradition is most energetically upheld by those students of the human fossil record who regard

virtually all fossil humans of the last 2 million years as members of *Homo sapiens* irrespective of what they actually look like and who seek the roots of today's major modern geographic groups of humans very deep in time.³ Any such interpretation of the remarkably diverse human fossil record known today involves giving primacy of place to considerations of time and geography and relegating morphology to a minor role at best.

Another factor contributing to this unusual situation is the reluctance of paleoanthropologists at large to move beyond a relatively fundamentalist adherence to the tenets of the "Synthesis" that came to dominate evolutionary biology during the 1950s. According to the Synthesis, virtually all evolutionary phenomena can be reduced to the shifting of gene frequencies in populations over vast periods of time under the action of natural selection (differential reproductive success).⁴ Since the early 1970s⁵ it has, however, been evident that the mechanisms of evolution are much more complex and varied than this gradualist model admits and that the mecha-

Dr. Tattersall is a curator in the Department of Anthropology at the American Museum of Natural History, New York City. He is especially interested in the integration of evolutionary theory with the fossil record and has worked most extensively on the lemurs of Madagascar and the human fossil record. His latest book is *Becoming Human: Evolution and Human Uniqueness* (Harcourt Brace, 1998). His fax number is 212-769-5334; his e-mail address is iant@amnh.org. Dr. Schwartz is Professor of Anthropology at the University of Pittsburgh and Research Associate at the American Museum of Natural History. His major research interest is in developmental processes and the systematics of fossil and living primates. He is the author of the forthcoming *The New Evolution: Fossils, Genes and the Origin of Species*. His fax number is 412-648-7535; his e-mail address is jhs+@pitt.edu

nisms of adaptive change and lineage splitting may in fact be quite distinct.⁶ Such considerations strongly suggest that we should abandon strictly linear models of human evolution and look instead for evidence of species diversity in the human fossil record. And this endeavor dictates in turn that paleoanthropologists begin to afford morphology the attention it deserves.

SPECIATION AND MORPHOLOGICAL CHANGE

In some ways giving morphology the attention it deserves is more easily said than done. Comparative surveys of the extant fauna show clearly that speciation, the process whereby a new species buds off from an old one to create a new lineage, is not simply an inevitable result of the accumulation, adaptive or otherwise, of morphological novelty.⁷ Instead, as we've suggested above, the processes lying behind morphological change and speciation are quite different. And the corollary of this is that there is no specifiable degree of morphological difference with which speciation is necessarily associated.⁷ For systematists (those whose business it is to catalog and classify diversity in the living world) who work with living creatures, this often is not a practical problem, for species are generally regarded as the largest reproductive units, so that reproductive behaviors and other properties can be invoked in determining species status. For paleontologists, however, the problem is acute, for morphology is the sole key to knowing whether two fossils that differ only slightly belong to the same or different species.

We thus have to be careful how we proceed. And we should always be careful not to confuse intraspecies variation in the morphological characters we are looking at with interspecies variation. But, by being excessively attentive to the former, paleoanthropologists have clearly been able to paint far too simplistic a picture of human evolution, minimizing the number of species recognized and conferring a spurious appearance of linearity upon the process. For example, it is routinely demanded that a particular anatomical condition be present in every specimen of a species

or that it never be found outside that species before it can be regarded as a characteristic of the particular species in question. Yet this is to misunderstand the very nature of variation itself. Every species is a close relative of another, living or extinct, because the process of speciation involves the establishment of reproductive isolation between a parent and a daughter population that formerly belonged to the same species. And examination of very closely related species among living mammals confirms that they rarely if ever differ hugely in the characters of the bones and teeth that are all we normally have to go on in fossils.⁸ In most characters, indeed, ranges of variation in parent/daughter or sister species will usually show much or even total overlap. Demonstration of such overlap in this or that character or even a set of characters is thus

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meaningless as an indicator of species identity. Similarly, even though normal within-population variation will include the nonexpression of certain characters (e.g., the anterior mastoid tubercle in some Neanderthals⁹), it entails a large loss of information to exclude such characters from consideration entirely. And, given the close genetic similarity of sister species, it would hardly be surprising that occasionally a morphological variant typical of one should exceptionally turn up in another.

What, then, is the paleontologist to do? Our own preference is to take what appears to us to be a rather conservative stance and to recognize the existence of separate species when distinct *morphs* (i.e., recognizable morphological entities distinguished by reasonably consistent sets of characters) are present in a fossil sample. We

recognize that in some cases real biological species (those distinguished by only minor morphological disparities) will escape recognition under this approach, but erring thus on the side of caution ensures that, while the actual phylogenetic picture will be simplified, it will not be materially distorted. In the rest of this article we apply this criterion to the Neanderthals, next to *Homo sapiens* incomparably the best known of all hominids.

THE NEANDERTHALS

The first to be discovered of all extinct hominid groups, the Neanderthals emerged as a distinct morphological entity at some point over about 200 thousand years (kyr) ago and became widespread over Europe and western Asia (from the Atlantic to Uzbekistan and from north Wales to the Levant) before their extinction after 30 kyr ago, presumably as a result of the incursion of modern humans into their home territory.¹⁰ The Neanderthals had brains as large as our own, which seems to be the primary factor influencing most paleoanthropologists of this half-century to include them in our own species, despite the fact that most mammalian genera contain multiple species with brains of essentially the same size. Those brains were, however, housed in crania of distinctly different shape from ours (Figs. 1, 2). Traditional lists of cranial differences of *Homo neanderthalensis* from *Homo sapiens* generally include the following: the hafting of the face in front of (rather than below) a long, low vault with relatively thick bone; the face itself large and protruding, with a very large nasal aperture and fossa (cavity) and curiously receding zygomatics (cheek bones); a distinct double-arched and smoothly rolled supraorbital torus (forehead ridge), continuous across the glabella (the surface just above the bridge of the nose); frontal sinuses with marked lateral expansion; undeveloped chin; thick, horizontal occipital torus; pitted suprainiac depression, with raised margins, in the midline above the torus; occipitomastoid process at least as salient as mastoid process; vaginal and mastoid processes not in contact; anterior mastoid tubercle present; chin lacking or poorly expressed; retromolar space present;

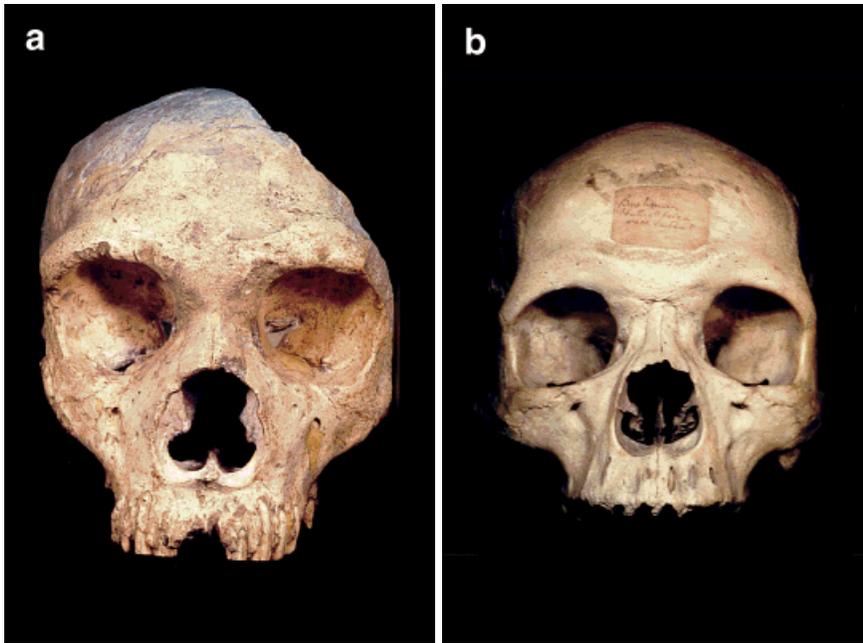


Fig. 1. Anterior view of two hominid skulls. **A.** Cranium of *Homo neanderthalensis* from the site of Gibraltar. Distinctively Neanderthal are the projecting snout and puffy lower face, the smoothly rolled brow that is continuous above the nasal region, the upwardly angled and posteriorly receding zygomatic arches, and the prominent medial projections within the large nasal aperture. The specimen is in the Natural History Museum, London. Photograph © Jeffrey H. Schwartz. **B.** Cranium of recent *Homo sapiens* (San, Africa). Compared to a typical Neanderthal, a modern human is itself distinguished by having a bipartite brow, which has a more bulging medial portion (minimally expressed in this specimen) and plate-like lateral extremities. *Homo sapiens* is primitive cranially, however, in the general configuration of the lower face, the zygomatic arches, nasal aperture, and conchae within the nasal cavity. This specimen is in the American Museum of Natural History, New York. Photograph © Jeffrey H. Schwartz.

etc. Above all, though, the general proportions of the skull and the relationship of its major areas to each other are quite distinct; and the Neanderthal postcranial skeleton boasts at least as many differences from us (*Homo sapiens*) as may be found in the skull. All in all, we have in the Neanderthals a morph that is undeniably distinct from that represented by *Homo sapiens* (as evidenced by the fact that it has been felt necessary to give them an informal name). At the very least, then, we have here a fully individuated hominid that requires to be recognized as its own species. Indeed, in the context of all human fossils known from Europe over the past half-million years or so, the evidence has long been available to show *Homo neanderthalensis* to have been simply the best-known component of a larger endemic European/western Asian clade (group of related species) that shares a common ancestry with our own African-derived clade but that has had a

separate evolutionary history for a considerable period of time.¹¹

When, a few years ago, we began our study of the Neanderthal and related fossil records, we naturally asked ourselves what we could possibly discover in these extinct hominids that had not been noticed in the almost century-and-a-half since the description of the first Neanderthal fossil. We rapidly discovered that a great deal of Neanderthal morphology had been neglected by paleoanthropologists, presumably because their adherence to a gradualist view of human evolution had made morphology secondary to considerations of time. Paleoanthropological opinion was (and to a dismayingly large extent still is) effectively divided between those who considered the Neanderthals to be the direct precursors of modern Europeans¹² and those who considered them to be no more than an unusual subspecies of *Homo sapiens*¹³ that was genetically swamped by the modern humans who

first entered Europe about 40 kyr ago. Significantly, adherence to either scenario renders detailed considerations of anatomy effectively superfluous.

It may be this that accounts for what we may reasonably consider the overreaction to the first of our discoveries relating to Neanderthal morphology. It has long been acknowledged that Neanderthal crania are distinguished by large nasal apertures and capacious nasal fossae, and indeed these features have long figured in speculations that these extinct humans were somehow “cold-adapted.”¹⁴ Yet, as far as we could determine, it had never been remarked that just within the Neanderthal nasal aperture reside some very unusual structures indeed—structures that are particularly evident in the Gibraltar skull (discovered before 1848), which happened to be the first Neanderthal fossil

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we examined (Fig. 3). In this individual there is a secondary internal margin to the bottom of the nasal aperture (itself occasionally present in modern humans) that expands superiorly (and uniquely) into a pronounced medial projection which partly occludes the entrance to the nasal fossa. Behind this medial projection, the lateral wall of the fossa expands markedly medially, yet further constricting the airway. There is no conchal crest marking the anterior articulation of the inferior nasal concha, as is found in *Homo sapiens* and in other species of *Homo*. In general, this conformation suggests a turbinate system totally unlike not only those of other hominids and other primates but also of all other mammals (if any reader knows of any parallels, we would be most interested to hear of them). The internal nasal region is commonly damaged in fossils, but we have subse-

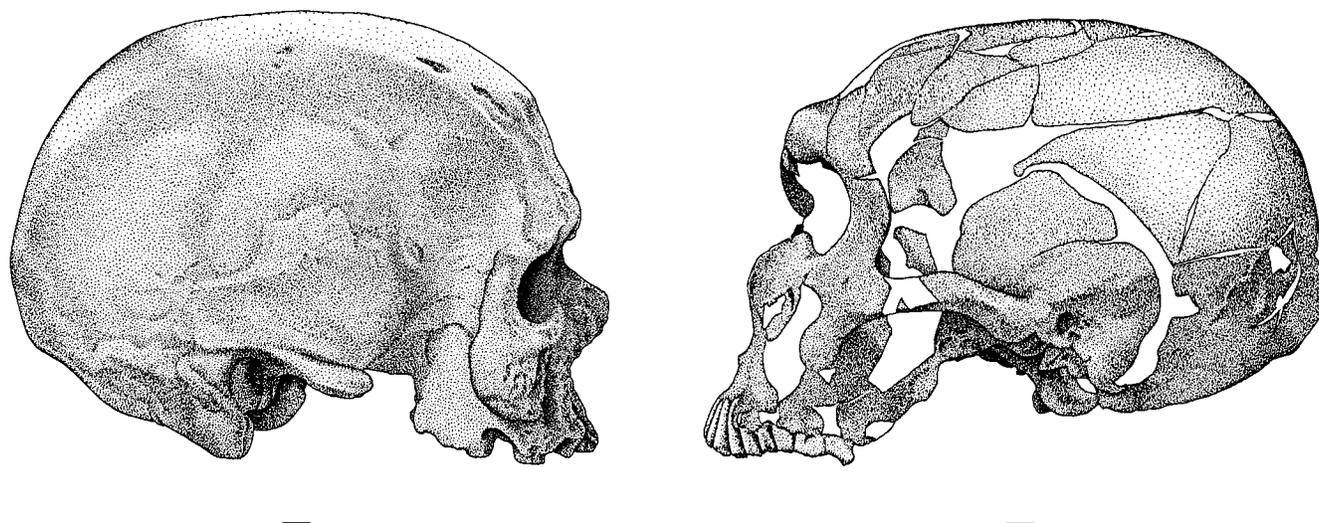


Fig. 2. Lateral view of an early modern human cranium (left) (Cro-Magnon, France) compared with that of a Neanderthal (right) (La Ferrassie 1, France). Scale bars = 1 cm. Drawings by Don McGranaghan.

quently observed this unusual nasal morphology in all Neanderthal fossils we have seen in which this region is preserved—although naturally there is some variation in the degree to which the medial projection is expressed.

An independent study has confirmed this peculiar conformation of the nasal fossa in Neanderthals,¹⁵ but, rather than welcoming this additional information about our closest well-known relatives, the paleoanthropological community, in a perhaps predictable reaction, has rejected it out of hand. Ironically, though, while one school has sought to invalidate our data by showing that medial projections do not exist in Neanderthals (R. Franciscus, personal communication), another has attempted to achieve the same end by showing that this morphology is actually present in *Homo sapiens*!¹⁶ In the event, neither demonstration is possible, for the morphology speaks for itself, and these denials are based on misidentification of the morphologies observed by the authors concerned.

While we welcome the opportunity to point this out, it seems to us that the larger issue is the more important one: attention to the details of comparative morphology (and the development of the characters compared) has been sorely neglected in paleoanthropology simply because the historical biases and evolutionary paradigms favored by paleoanthropologists have at some

level made morphology superfluous to their enterprise. It is not altogether unrealistic to conclude that today many believe that the Neanderthals are unusual *Homo sapiens* at least in part because in the preevolutionary days of 1856 Hermann Schaaffhausen, the describer of the original Neanderthal fossil, had no option to think otherwise; and it is also fair to observe that many paleoanthropologists proceed as if phylogenetic analysis were mainly an exercise in joining up points on a stratigraphic chart.

On the systematic level, this insularity is thrown into dramatic relief by the energy expended in (so far unsuccessful) attempts to find one or two examples of Neanderthal-like medial projections among the many thousands of modern human crania represented in museum collections.¹⁶ The fundamental point here is not that it might potentially be possible to find an example of a Neanderthal morphology in a modern *Homo sapiens* (as has indeed been inaccurately claimed in the case of the skull rears of some very early modern Europeans, e.g. Mladec¹⁷). If so, so what? The point is that both *Homo neanderthalensis* and *Homo sapiens* are variable and that, crucially, they vary around very different means, even were a point or two of overlap to be identified. In short, moderns and Neanderthals are variations on two distinctly different

themes, and we should recognize them as such.

Interestingly, the remarkable sequencing of 378 kb of mtDNA from the hypervariable region I of the original Neanderthal (Feldhofer) fossil (probably between 50 and 100 kyr old) has shown this individual to be a very distant outlier when compared to all modern human populations.¹⁸ Further, the researchers involved estimated that the Neanderthal and *Homo sapiens* lineages diverged as long ago as around 600 kyr—an estimate also quite reasonable on morphological grounds.¹⁹ In an age of technophilia, one might have expected that this compelling evidence should force rethinking about the status of the Neanderthals as a distinct species. Alas, no. Supporters of linear models of human evolution were as quick to reject this new category of information as reflexively as they had rejected morphology.²⁰ The argument thus continues, as listlessly as before.

Yet in our view it is crucially important not to write off the Neanderthals as bizarre or inferior versions of *Homo sapiens*. The Neanderthals are a major presence in the human fossil record not because they are the source from which *Homo sapiens* sprang, for certainly they are not, but because they are incomparably better known archaeologically than any other extinct hominid species. In this sense, they are the best yardstick we have by

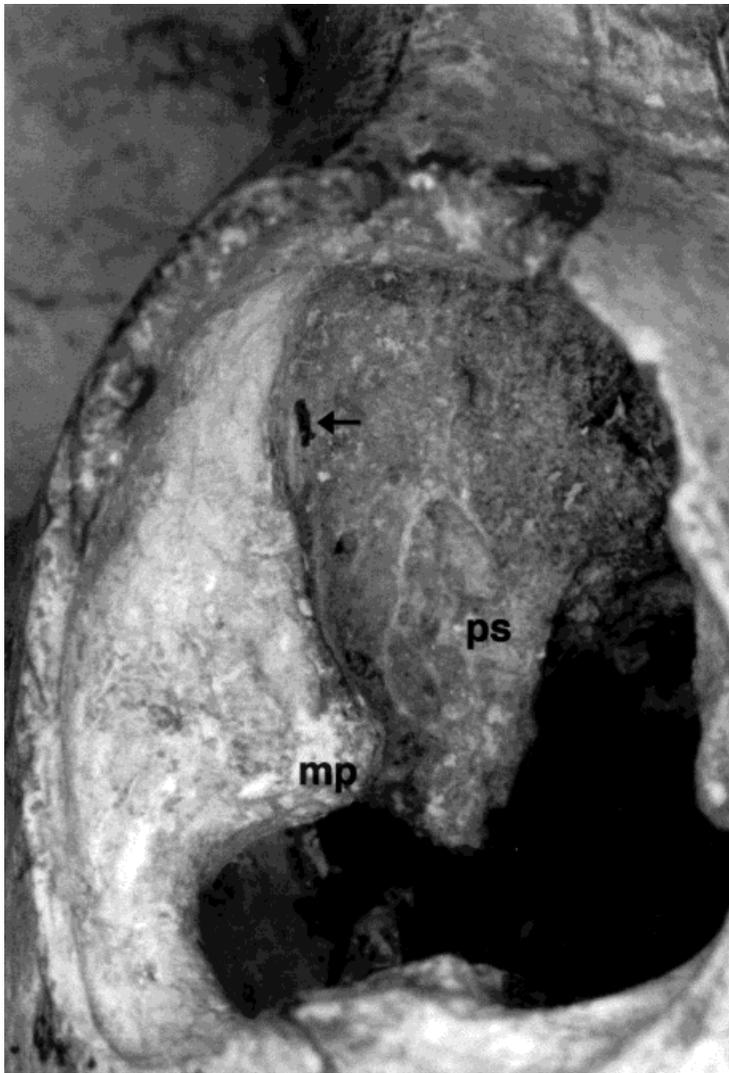


Fig. 3. View of the right wall of the nasal fossa in the Gibraltar Neanderthal cranium showing the internal margin that enlarges above into the medial projection (mp). Behind this is seen evidence of the posterior swelling (ps), partly obscured in this view by matrix. The arrow indicates the hole in the wall of the swelling that reveals the enlarged maxillary sinus. Photo © Jeffrey H. Schwartz.

which to measure our own uniqueness, for the archaeological record of the Neanderthals shows that they were creatures of another order from us who dealt with the world in a very different way.⁶ It is wrong to feel that excluding the Neanderthals from *Homo sapiens* is reprehensible discrimination, for in reality quite the reverse is true. We can do these remarkable extinct humans justice only if we regard them as an evolutionary phenomenon in their own right, a phenomenon that demands understanding and explanation in its own

terms. And if we are to achieve such justice as well as a reasonable perspective on diversity in the human fossil record, we have to restore morphology to its rightful place of primacy in the analysis of that record.

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