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Commentary

What the nose knows: New understandings of Neanderthal upper respiratory tract specializations

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Who were the Neanderthals? This brief question has been at the heart of paleoanthropology since the unearthing of the first Neanderthals almost a century and a half ago. First found at sites in western Europe, such as the Neander "thal" or valley in Germany, Gibraltar, Spy in Belgium, or La Chapelle-aux-Saints in France, these peculiar remains continue to be an enigma (1, 2). Were they mere variants of living human populations, somewhat different so as to indicate a distinct "race," or were they imbued with sufficient uniquely derived characters (autapomorphies) so as to warrant their own species, *Homo neanderthalensis*? Although it is generally agreed that Neanderthals existed for about 200,000 years before their disappearance some 30,000 years ago and that they inhabited a range including much of Europe, western Asia, and the Levant, much disagreement remains as to what their phylogenetic affinities were. For example, did Neanderthals and living humans both arise from an early group of *Homo sapiens* some 300,000–400,000 years ago or did Neanderthals arise separately from some pre-*sapiens* group much earlier in the Pleistocene? And, of course, what happened to them? Although questions abound, definitive answers are few.

A confounding problem in the search to understand the Neanderthals, as with hominid ancestors in general, is that important aspects of their functional morphology and underlying behaviors have gone largely underinvestigated. This, in part, is because paleoanthropologists have had to focus upon the scant bony remains available to them, remains which often do not reflect some major biological systems. For example, although aspects of the dentition or postcranial skeleton have been reconstructed meticulously, others, such as features of the respiratory, digestive, or nervous systems have, more often than not, either been ignored or relegated to a relatively minor role in discussions.

The recent observations by Schwartz and Tattersall (3), in this issue of the *Proceedings*, on Neanderthal nasal apomorphies shed new light on the relationship of Neanderthals to other hominids and add important new data for our understanding of the functional morphology of a major physiologic system, the upper respiratory tract. The authors' primary interest is, of course, how these newly described features will affect the interpretation of Neanderthal phylogeny. To be fair, the position of Schwartz and Tattersall on this issue is well known among anthropologists, with both recognized as "splitters" who see Neanderthals as comprising a distinct species from either living or archaic *Homo sapiens* (1, 4, 5). Their prior views notwithstanding, the evidence they present is of value in its own right and will henceforth have to be factored into any discussion of Neanderthal relationships.

The findings by Schwartz and Tattersall regard specializations of internal nasal morphology. This aspect of the nose has gone largely unexplored in our fossil ancestors. This is because fragile internal nasal structures are often not preserved in fossil hominids and because many aspects of the functional morphology underlying the mammalian nose and associated paranasal sinuses remain poorly understood. Although accounts of internal nasal morphology have been cursory, there have been studies on external nasal dimensions of both extant and fossil hominids (6–9). Indeed, the large size of Neanderthal external nasal dimensions, and the significant differences they exhibit from those of extant humans, has been commented upon and documented for some time (10–12). Schwartz and Tattersall now bring to the discussion three internal nasal features which have been previously unrecognized and which they feel are autapomorphic to Neanderthals: (*i*) an "internal nasal margin," a medially projecting rim of bone just within the anterior edge of the anterior nasal (piriform) aperture; (*ii*) a pronounced medial swelling of the lateral nasal wall; and (*iii*) a lack of an ossified roof over the lacrimal groove.

Should the features observed by Schwartz and Tattersall indeed prove to be true apomorphies, they would provide strong evidence to support the contention that Neanderthals are different from extant or fossil *Homo sapiens* in seminal ways. But in what ways? And what do distinctions in their nasal region reflect? While focusing upon questions of Neanderthal systematics, Schwartz and Tattersall have led us to ponder pivotal questions about how the Neanderthals may have differed from us in aspects of their respiratory tract and constituent behaviors.

The acquisition and processing of oxygen and its byproducts is the primary mission of any air-breathing vertebrate. Chewing, walking, reproducing, thinking are all fine, but first one has to breathe. Anthropologists sometimes seem to forget this; evolution never does. Although most of anthropology has focused upon the more direct evidence of our past, some workers have attempted to reconstruct the evolutionary aspects of our more elusive respiratory behaviors. This work has focused largely on reconstructing the upper respiratory, or aerodigestive, tract and has been principally concerned with establishing what the overall positioning of structures such as the larynx, tongue, and pharynx may have been like in hominid ancestors. Our own studies (13–16) among others (17–19) have shown that aspects of the external contour of the skull base are intimately related to the topographic arrangement of aerodigestive tract structures and can, in turn, serve as a guide to help reconstruct the anatomy of the region in our ancestors. In essence, we have learned that the basicranium is the "roof" of the upper respiratory tract and that it can serve as a blueprint from which the "house" below can be re-created. By coupling these data on how upper respiratory tract structures can be reconstructed with our growing knowledge of the comparative and functional anatomy of this region in extant mammals (20, 21), we have begun to gain insight into what the upper respiratory tract may have been like in ancestors as far back as Plio-Pleistocene australopithecines (22).

The configuration of this region in Neanderthals has been the subject of thought beginning, at least, with the great anatomist Sir Arthur Keith (23). The focus, however, has usually not been on respiratory requirements and related behaviors but, rather, on the "vocal tract" component. Although few studies wrestle with the key issues of upper respiratory change, it seems as if almost everyone has a word to say on what a Neanderthal's vocal tract may have been like.

Although the question of Neanderthal speech capabilities is indeed intriguing, this allure has seemingly caused many to lose sight of what the area's main functions were: respiration and, secondarily, ingestion of food. The region did not evolve for the sole purpose of vocalization, a fact often overlooked by many.

The general picture of the Neanderthal upper respiratory tract that has emerged over the last few decades by those attempting to reconstruct it has been of a region which differed somewhat from that in living humans. Both our own (15, 16, 24) and other studies (17, 18, 25) have emphasized that some Neanderthals (such as the "Classic" western European specimens) would have exhibited a larynx slightly higher in the neck than that of modern humans, with these Neanderthals having a more limited oropharyngeal segment with a greater portion of the tongue occupying the oral cavity. When one factors in their large external nose and sizable paranasal sinuses, the overall Neanderthal anatomy suggests a group that relied more heavily upon the nasal rather than the oral route for respiration then do living humans. These specializations were very possibly due to respiratory-related adaptations to their environment. A by-product of this respiratory-driven anatomical configuration would be that Neanderthals could not have produced the same array of sounds that living humans can (16, 17, 26). They were not apish mutes; they were just not identical to us.

Although the above scenario has been accepted by many, it is unpalatable to some. This group, often called "lumpers," is primarily comprised of those who view Neanderthals as falling within the range of variation represented by diverse modern human populations (27). Given their predilection, it becomes *a priori* impossible for them to view Neanderthals as ever being sufficiently different so as to exhibit highly derived respiratory anatomy or specialized respiratory or vocal behaviors. If they are us, then they cannot be fundamentally different. Observations on the difference between Neanderthals and extant populations are routinely dismissed as being within the range of "human" variation.

Given the above, Schwartz and Tattersall's nasal findings harbor important implications. The three traits they describe clearly suggest a morphology that is different from ours and appears designed to subserve specialized functions. The large internal nasal margin they describe, their major observation, may serve to expand the internal surface area, thus allowing for an increase in ciliated mucosal covering. The placement of this margin, at the very entrance of the cavity, also suggests a location ideally suited to be the initial vehicle to confront inspired air or the last opportunity to interact with expired air. In some ways, this medial projection is reminiscent of Waldeyer's Ring, the mucosa-associated lymphoid tissues (lingual, palatine, nasopharyngeal tonsils) that surround internal respiratory and digestive portals. Could Neanderthals have had a similar "donut-shaped" filter system at the entrance to the nasal cavity?

Both the internal nasal margin and Schwartz and Tattersall's second feature, a swelling of the lateral nasal cavity, may be related to expansions of the paranasal sinus system. Indeed, sinuses have long been known to be extensive in Neanderthals (28), and amplifications of these would thus be logical. Although the exact function(s) of mammalian paranasal sinuses remains unclear, and have indeed become the focus of much recent study (29–31), it is likely that in Neanderthals they played at least some part in an air-exchange process, perhaps in warming and humidifying cold and dry air. The relationships/functions of an unossified roof over the lacrimal groove, Schwartz and Tattersall's third observation, is less clear. The absence of a rigid roof, however, would clearly permit more expandability for components of the nasolacrimal duct system (which, in humans, contains a venous plexus forming erectile tissues and can, when engorged, obstruct the duct). Absence of a bony roof would also allow for a more direct communication of nasolacrimal duct contents with the environment of the nasal cavity proper.

As an initial foray into this region in Neanderthals, many questions have yet to be addressed. An important issue, not covered by Schwartz and Tattersall, regards the extent (or even presence) of these proposed apomorphies in Neanderthals from different geographic areas. For example, because the Neanderthals focused on by the authors are from western Europe, it will be important to determine the extent of these characters in Neanderthals from other areas, such as eastern Europe or the Levant. If regional variations are found, could there be any relationship to climatic differences? Similarly, further work is needed to determine when these characters began to appear in the Neanderthal lineage, and whether, as the authors suggest, the presence of a "poorly developed" medial projection in the Steinheim cranium (a specimen generally thought not to be a Neanderthal) is evidence for an entire Neanderthal clade.

The apomorphies described by Schwartz and Tattersall offer strong evidence that the internal morphology of the nasal moiety of the Neanderthal upper respiratory tract may be as distinctive as that previously reconstructed for the more caudal laryngo-pharyngeal component. Taken together, these specialized features of different upper respiratory tract compartments allow greater insight into an apparently more global pattern to Neanderthal upper respiratory specializations. Although these specializations may not by themselves validate Schwartz and Tattersall's preference for Neanderthal taxonomic distinctiveness, they certainly lend strong support to those who see Neanderthals as considerably different from living *Homo sapiens*. Indeed, further clues to understanding just how different Neanderthals are from living humans may be as plain as the anatomy inside the noses on their faces.

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