# Neandertal nasal structures and upper respiratory tract "specialization"

(human evolution/Late Pleistocene/nasal morphology)

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**ABSTRACT** **Schwartz and Tattersall [Schwartz, J. H. & Tattersall, I. (1996)** *Proc. Natl. Acad. Sci. USA* **93, 10852–10854] have argued for a previously unrecognized suite of autapomorphies in the internal nasal region of Neandertals that make them unique, not only among hominids, but possibly among all other terrestrial mammals. These purported autapomorphies include (***i***) the development of an internal nasal margin bearing a well developed and vertically oriented medial projection; (***ii***) a pronounced medial swelling of the lateral nasal wall into the posterior nasal cavity; and (***iii***) the lack of an ossified roof over the lacrimal groove. In addition, Laitman** *et al.* **[Laitman, J. T., Reidenberg, J. S., Marquez, S. & Gannon, P. J. (1996)** *Proc. Natl. Acad. Sci. USA* **93, 10543–10545] pointed to these features as evidence for upper respiratory tract specializations among the Neandertals, indicating potential differences in behavior compared with modern humans. Critically reviewing the anatomical basis for Schwartz and Tattersall's contentions reveals several serious problems with their analysis, including (***i***) reliance on specimens with damaged, incomplete, or, in some cases, entirely absent relevant anatomy; (***ii***) failure to consider primary vs. secondary spatial consequences in nasal trait conceptualization; and (***iii***) failure to consider actual ranges of variation in these traits in both fossil and recent humans. Accordingly, the unique phylogenetic and adaptive "specializations" attributed to Neandertal internal nasal structures are unwarranted.**

The recent recovery and sequencing of mtDNA from the Feldhofer Cave Neandertal (1) has provided a significant new technical twist on the oldest debate in paleoanthropology: the role of Neandertals in the evolution of modern humans. The methodological aspects of this widely cited study have not been criticized. Predictably, however, there has been divided opinion (2, 3) on the interpretations of the results, namely, those indicating that modern humans arose recently in Africa as a separate species and replaced the Neandertals, a distinct lineage with substantial time depth in Europe, with essentially no interbreeding. It seems clear that ongoing refinements in genetic analyses will continue to provide important new information on this debate. However, it is also apparent that there remains a relatively wide gap between theory and data in molecular evolutionary studies (4) and that both paleontological and archaeological data will remain important in the ongoing discussion of modern human origins.

The paleontological basis for deciphering Neandertal–modern human relationships has centered heavily on the identification of unique Neandertal traits or autapomorphies. Recently, Schwartz and Tattersall (5) have drawn attention to what they consider a previously unrecognized suite of autapomorphies in the internal nasal region of Neandertals that make them unique, not only among hominids, but possibly among all other terrestrial mammals. These purported autapomorphies include (*i*) the development of an internal nasal margin bearing

a well developed and vertically oriented medial projection; (*ii*) a pronounced medial swelling of the lateral nasal wall into the posterior nasal cavity; and (*iii*) the lack of an ossified roof over the lacrimal groove. Beyond providing phylogenetic valence, these autapomorphies were presented as evidence for a radical reorganization of internal nasal anatomy among Neandertals, reflecting upper respiratory tract specializations that suggest key differences in behavior compared with modern humans (6). These wide-ranging and widely cited conclusions were based on a small sample of the available fossil remains. The purpose of this report is to evaluate these observations and interpretations critically, in light of a wider and more comprehensive study of the internal and external nasal region of over 200 Pleistocene adult and subadult fossil hominids, including most of the available Neandertal remains, and 523 geographically varied recent humans from the western Old World (7).

**The Internal Nasal Margin and Medial Projection.** The "[m]ost striking" trait that Schwartz and Tattersall (5) identified is "a rim of raised bone that projects from either side of the rim of the anterior nasal aperture just within its anterior edge, forming a secondary 'internal margin.' This rim runs one-third to halfway up the inner nasal wall on both sides and then expands to become a wide, broad-based and bluntly pointed mass that protrudes medially into the nasal cavity." According to the authors, the feature is particularly evident in the Forbes' Quarry skull. The feature is also labeled on a photo of Spy 1 in their article, and was observed further on La Ferrassie 1, La Chapelle-aux-Saints, St. Césaire, and in a published photo of Shanidar 1. Furthermore, according to the authors, "[a]lthough the conchal crest of extant mammals . . . , including *Homo sapiens* . . . , occurs in the same general area within the nasal cavity as the medial prominence does in these Neanderthals, it arises farther back and is horizontal rather than vertical in orientation."

The internal nasal margin that Schwartz and Tattersall (5) identified has been known since at least the end of the last century (8, 9). Since then, the nomenclature most frequently used for this trait is crista turbinalis, as named by Gower (10), who defined this narial margin as a ridge arising near the anterior end of the inferior turbinal that can course as far inferiorly and medially as the median line (incisor crest–anterior nasal spine). The crista turbinalis can be a distinct entity, or it can merge with one or both of the crista spinalis (a ridge arising from the anterior nasal spine) and the crista lateralis (a ridge arising as an extension of the lateral edge of the apertura piriformis). There is considerable variation in the precise manifestation of these crests in recent humans and fossil hominids, although most workers, including the most recent (7, 11, 12), have used some variation of Gower's (10) Stage 1–6 coding protocol.

Far from being unique to Neandertals, as Schwartz and Tattersall (5) maintained, the crista turbinalis is present in the

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Table 1.  Frequency of internal nasal rim (crista turbinalis) and Stage 5 narial margin*

| Sample | n | Crista turbinalis, % | Stage 5, % |
|---|---|---|---|
| Non-Neandertal, Archaic | 18 | 94.4 | 0.0 |
| Neandertals | 20 | 76.9 | 65.0 |
| European, Early Modern | 21 | 66.8 | 4.8 |
| European, Late Modern | 19 | 57.9 | 0.0 |
| Western European, recent | 112 | 60.8 | 18.8 |
| Central European, recent | 109 | 46.9 | 2.8 |
| Near Eastern, recent | 72 | 40.4 | 11.1 |
| North African, Mesolithic | 68 | 55.9 | 11.8 |
| North African, recent | 68 | 50.1 | 5.9 |
| African, Early Holocene | 9 | 77.7 | 0.0 |
| African Bantu, recent | 119 | 82.7 | 15.1 |
| African Khoisan, recent | 43 | 86.1 | 7.0 |

*The terminology follows Gower's nomenclature (10); the data are from ref. 7.

internal aspect of the apertura piriformis in high frequencies in most recent humans and fossil *Homo*, especially those from Africa (Table 1). Moreover, the precise configuration of all three cristae, when present, found in 65% of Neandertals (Gower's Stage 5: fused cristae lateralis and spinalis with partial fusion of cristae spinalis and turbinalis) can be found in more than 10% of recent samples from western Europe, the Near East, and sub-Saharan Africa, as well as a north African Mesolithic (Taforalt and Afalou) and Nubian Mesolithic (Jebel Sahaba) sample (Table 1). It is important to point out that 35% of the Neandertal sample does not have an internal margin or a crista turbinalis, possessing instead a single, sharp crest that is continuous between the anterior nasal spine and the lateral walls of the apertura piriformis. These include Amud 1, Amud 7 (subadult), Arcy-Sur-Cure 9, St. Césaire 1, Spy 1, and possibly Teshik Tash (the last was observed from a cast).

Schwartz and Tattersall's (5) description of the medial projection as a Neandertal autapomorphy is also dubious. There is no dispute that the root for the conchal crest is visible in an anterior view in many Neandertals. The problem is that the conchal crest is also visible in many other non-Neandertal premodern fossils and in recent humans to varying degrees. In recent humans, the conchal crest is especially visible in samples characterized by relatively wide mean values for the apertura piriformis. An alternative explanation for the "medial projection" of the conchal root in all hominids that exhibit this configuration is greater lateral placement of the lateral borders of the apertura piriformis. There are at least two reasons that the conchal root may appear to be accentuated in some (although not all) Neandertals. First, on average, Neandertals retain wide nasal (or apertura piriformis) breadths, common in all earlier hominids (Table 2), as a retained primitive trait for *Homo*. In addition, Neandertals show marked anterolateral eversion of the frontal processes of the maxillae, a derived condition that is spatially tied to other zygomaticomaxillary autapomorphies that are well known and were first documented in detail over 50 years ago (13). This condition results in an apertura piriformis that is wide not only in the lower middle portion (common in many other hominids) but in the superior portions as well (a derived condition), resulting in an overall larger and more square rather than pear-shaped apertura piriformis. This feature can be quantified by comparing the distance across the inferior nasal bones at the superior apertura piriformis (Table 3). Note that among earlier hominids, only Atapuerca SH5 approximates the mean absolute width for Neandertals, and the Neandertals are significantly wider than all other samples. When inferior nasal bone width is standardized to the breadth of the apertura piriformis, Neandertals again have the highest value (higher ratio values

Table 2.  Nasal breadth (M54; ref. 20)

| Sample | n | Mean, mm | SD, mm |
|---|---|---|---|
| Non-Neandertal, Archaic | 13 | 33.4 | 4.3 |
| Neandertals | 14 | 32.4 | 3.2 |
| European, Early Modern | 23 | 26.0* | 2.1 |
| European, Late Modern | 13 | 23.8* | 2.0 |
| Western European, recent | 112 | 23.4* | 1.9 |
| Central European, recent | 109 | 24.0* | 1.8 |
| Near Eastern, recent | 72 | 24.2* | 2.3 |
| North African, Mesolithic | 30 | 27.4* | 2.1 |
| North African, recent | 68 | 24.1* | 2.0 |
| African, Early Holocene | 8 | 26.0* | 2.3 |
| African Bantu, recent | 119 | 27.1* | 2.1 |
| African Khoisan, recent | 43 | 25.8* | 2.1 |

*, $P < 0.05$ (significant differences from the Neandertal mean).

indicate more square aperturae piriformis, and lower values more pear-shaped).

Given these results, the roots for the conchal crest appear to be more medially placed only in some specimens, as a secondary consequence of wider aperturae piriformis breadths (the primary trait) and will be even more pronounced in some

Table 3.  Inferior nasal bone width (INBW; M57.3; ref. 20) measured absolutely and relative to nasal breadth (NLB; M54; ref. 20)

| Specimen/Sample | INBW, mm | INBW/NLB, % |
|---|---|---|
| Non-Neandertal Archaic | | |
| KNM-ER 3733 | 17.8 | 49.4 |
| KNM-WT 15000 (subadult) | 23.8 | 67.4 |
| Bodo (cast) | 23.0 | 54.1 |
| Kabwe 1 | 19.1 | 62.8 |
| Atapuerca SH5 (ref. 19) | 25.0 | 64.9 |
| Petralona 1 | 21.0 | 57.7 |
| Qafzeh 6 | 18.0 | 55.7 |
| Neandertals | | |
| La Chapelle-aux-Saints 1 | 22.8 | 68.7 |
| La Ferrassie 1 | 33.0 | 96.2 |
| Gibraltar 1 | 20.5 | 61.0 |
| Guattari 1 | 26.6 | 76.0 |
| Krapina 3† | (24.0) | (85.7) |
| La Quina 18 (subadult) | 18.9 | 84.4 |
| Roc de Marsal 1 (subadult) | 16.0 | 73.1 |
| Saccopastore 1 | 24.1 | 77.2 |
| Saccopastore 2 | 29.0 | 86.3 |
| Subalyuk 2 (subadult)† | (16.2) | (85.3) |
| Shanidar 5 (cast) | 23.0 | (59.7) |
| Tabun C1† | (25.2) | (74.1) |
| Teshik Tash (cast, subadult) | (27.0) | (87.1) |

| | n | Mean, mm | SD, mm | Mean, % | SD, % |
|---|---|---|---|---|---|
| Adult Neandertals | 9 | 25.4 | 3.7 | 76.1 | 12.0 |
| All Neandertals | 13 | 23.6 | 4.9 | 78.1 | 10.8 |
| European, Early Modern | 14 | 17.7* | 2.1 | 70.2 | 6.5 |
| European, Late Modern | 8 | 16.8* | 1.7 | 72.9 | 6.3 |
| Western European, recent | 112 | 16.4* | 2.0 | 70.0* | 7.4 |
| Central, European, recent | 109 | 16.5* | 1.9 | 68.6* | 6.8 |
| Near Eastern, recent | 72 | 16.1* | 2.1 | 66.3* | 6.8 |
| North African, Mesolithic | 20 | 20.1* | 2.9 | 73.5 | 10.0 |
| North African, recent | 68 | 16.1* | 1.7 | 66.8* | 5.7 |
| African, Early Holocene | 7 | 15.7* | 4.0 | 60.4* | 14.1 |
| African, Bantu, recent | 119 | 17.9* | 1.9 | 66.2* | 6.7 |
| African Khoisan, recent | 43 | 15.5* | 2.4 | 60.1* | 7.6 |

All measurements taken on originals by the author unless otherwise noted. Parentheses indicate slight estimation. *, $P < 0.05$ (significant differences from the Neandertal adult mean).
†Value doubled from midline.

Neandertals. These considerations illustrate three important potential problems in the application of cladistics at low taxonomic levels: (*i*) failure to distinguish between primary and secondary spatial determinants of character presence/absence; (*ii*) the likelihood that many, if not most, "discrete" traits actually manifest along a metric continuum; and (*iii*) the importance of sampling widely to circumscribe realistic ranges of variation (14, 15, 16).

With respect to Schwartz and Tattersall's (5) contention that the conchal crest is oriented vertically rather than horizontally in Neandertals, the two specimens used in their article as photo illustrations of this feature are problematic. Spy 1 is missing the area of the lateral wall of the maxilla where the conchal crest (and thus the purported projection) would be located. The feature labeled in their photograph of this specimen (their figure 2a) as the medial projection is, in reality, the confluence of the cristae lateralis and spinalis on what remains of the inferolateral corner of the apertura piriformis. The degree of horizontality vs. verticality of the conchal crest as well as the degree of medial projection cannot be determined for this specimen. This observation highlights another troublesome aspect of their analysis, namely, the inclusion of specimens that simply are missing relevant anatomy. Skhul V was included in their comparative sample (included in their table 1 as "*Homo sapiens* (?)"). However, there is not a single aspect of external or internal nasal anatomy present on this specimen; the entire midface is restored in plaster. It is also unclear which features the Neandertal Gibraltar 2 (Devil's Tower) specimen evinces, because it is also missing the areas necessary to evaluate the purported inner margin, medial projection, or lacrimal groove (see below).

The Gibraltar 1 (Forbes' Quarry) Neandertal specimen was emphasized heavily by Schwartz and Tattersall (5) but is also problematic. Before cleaning with a pneumatic drill, the internal nasal fossa of this specimen was filled in completely with a hard breccia. It is not at all clear whether the present form of the medial projections in this specimen (the most pronounced among all of the Neandertals) is the result of "pneumatic sculpting" or actual anatomy. My own measurements on this and other aspects of the specimen (see below) are placed in parentheses to reflect this uncertainty. In specimens such as La Chapelle-aux-Saints, where the root of the conchal crest has not been damaged heavily, its orientation is clearly horizontal/oblique rather than vertical.

**Medial Swelling of the Lateral Nasal Wall into the Posterior Nasal Cavity.** Schwartz and Tattersall (5) argued for a second autapomorphy based on the Gibraltar 1 and Spy 1 specimens, namely a swelling of the lateral nasal cavity wall into the posterior nasal cavity. In a note added in proof, they also pointed to this feature in the Kulna specimen. According to the authors,

> this observation suggests that the Neanderthals were specialized in the posterior as well as the anterior nasal region relative to other terrestrial mammals. . . , including *Homo sapiens*. In the more general (and almost certainly primitive) configuration exemplified by the latter, there is no medial swelling of the posterolateral wall of the nasal cavity. The nasal cavity of extant terrestrial mammals is normally filled to varying degrees. . . with two, three, or even four pairs of turbinates that derive and swell laterally from the ethmoid bone that lies in the midsection of the cavity wall, and given the peculiar nasal morphology of Neanderthals, it appears likely that the turbinates of these extinct hominids, and possibly also the ethmoid, were configured in an unusual manner.

Direct measurements of internal nasal breadth were taken between the lateral internal nasal walls by using a specialized

internal dial caliper in six adult Neandertals, earlier and later fossil hominids, and a large series of geographically varied recent human samples. These measurements fail to support this purported autapomorphy as well (Table 4). Logically, a bilateral swelling of the Neandertal internal nasal wall would encroach on the available space in the internal fossa, leading to a narrower internal nasal-fossa breadth. Mean internal nasal-fossa breadth varies on average from 28.3 mm (European late-modern humans) to 37.9 mm for a mixed sample of Middle/Late Pleistocene hominids. Neandertals, at 34.5 mm, fall between these values and are virtually identical in mean value to several recent comparative samples. When internal nasal-fossa breadth is standardized to internal nasal-fossa length, Neandertals fall toward the low end of the index range but still are surpassed in narrowness by early and late modern European human samples and identical in relative breadth on average to the north African Mesolithic sample (Table 4).

As an additional check on this second purported autapomorphy, the breadth of the posterior nasal aperture (choanal breadth) also can be compared metrically (Table 5). Here again, Neandertals are narrower in this measurement compared with three Middle/Late Pleistocene specimens but not compared with all other modern human samples. In fact, European early modern humans on average have significantly narrower posterior nasal apertures than the Neandertals. Thus, based on a much wider array of comparisons and more objective measures for this purported trait, its autapomorphic status is also clearly rejected.

**Lack of an Ossified Roof over the Lacrimal Groove.** The final purported Neandertal autapomorphy that Schwartz and Tattersall (5) have identified is the lack of an ossified roof over the lacrimal groove, in contrast to modern humans in which the

Table 4. Internal nasal fossa breadth (INFB; ref. 7) measured absolutely and relative to internal nasal fossa length (INFL; ref 7)

| Specimen/Sample | INFB, mm | INFB/INFL, % |
|---|---|---|
| Non-Neandertal Archaic | | |
| Kabwe 1 | 40.0 | 50.0 |
| Kabwe 2 (E 687)† | (46.0) | — |
| Eliye Springs | (34.3) | — |
| Petralona 1 | (36.5) | (41.0) |
| Qafzeh 6 | (28.0) | — |
| Skhul 4 | 42.8 | — |
| Neandertals | | |
| Arcy-sur-Cure 9 (cast) | (35.0) | — |
| La Chapelle-aux-Saints 1 | 34.0 | 36.8 |
| Gibraltar 1 | (35.0) | (41.9) |
| Guattari 1 | 39.0 | 43.3 |
| Krapina 47 | 39.6 | — |
| Vindija 225 (cast)† | (30.0) | — |
| Vindija 259 (cast)† | (29.0) | — |

| | n | Mean, mm | SD, mm | Mean, % | SD, % |
|---|---|---|---|---|---|
| Neandertals | 7, 3 | 34.5 | 4.0 | 40.7 | 3.4 |
| European, Early Modern | 11, 2 | 30.7* | 3.8 | 40.4 | 8.1 |
| European, Late Modern | 10, 4 | 28.3* | 2.3 | 39.0 | 5.8 |
| Western European, recent | 112 | 32.7 | 3.3 | 43.6 | 4.8 |
| Central, European, recent | 109 | 35.0 | 3.5 | 47.4* | 5.7 |
| Mediterranean Near East, recent | 72 | 34.7 | 3.5 | 46.0 | 4.9 |
| North African, Mesolithic | 9, 3 | 30.7* | 2.7 | 40.7 | 2.3 |
| North African, recent | 68 | 32.6 | 3.0 | 44.0 | 4.6 |
| African, Bantu, recent | 119 | 34.3 | 4.1 | 49.7* | 6.7 |
| African Khoisan, recent | 43 | 33.8 | 3.9 | 51.6* | 5.4 |

All measurements taken on originals by the author unless otherwise noted. Parentheses indicate slight estimation. The first value for *n* is for INFB; the second value for *n* is for INFB/INFL. *, $P < 0.05$ (significant differences from the Neandertal mean).
†Value doubled from midline.

Table 5.   Posterior nasal fossa (choanal) breadth (M59.1; ref. 20)

| Specimen/Sample | | PNFB, mm | |
|---|---|---|---|
| Non-Neandertal Archaic | | | |
| Eliye Springs | | (33.0) | |
| Kabwe 1 | | 30.5 | |
| Petralona 1 | | 35.0 | |
| Neandertals | | | |
| Gibraltar 1 | | 27.5 | |
| Guattari 1 | | 26.2 | |
| Saccopastore 1 | | 26.2 | |
| Saccopastore 2 | | 28.6 | |
| | *n* | Mean, mm | SD, mm |
| Neandertals | 4 | 27.1 | 1.2 |
| European, Early Modern | 4 | 24.5* | 1.2 |
| European, Late Modern | 6 | 26.1 | 1.8 |
| Western European, recent | 112 | 26.7 | 2.5 |
| Central, European, recent | 109 | 27.6 | 2.3 |
| Mediterranean Near East, recent | 72 | 27.7 | 2.1 |
| North African, recent | 68 | 26.3 | 2.4 |
| African, Bantu, recent | 119 | 27.9 | 2.5 |
| African Khoisan, recent | 43 | 26.1 | 2.7 |

All measurements taken on originals by the author. Parentheses indicate slight estimation. *, $P < 0.05$ (significant differences from the Neandertal mean).
†Value doubled from midline.

lacrimal groove is roofed-over in adults and partially so in newborns. As with the other two features, however, no modern comparative sample is specified other than Skhul V (which completely lacks any preserved nasal anatomy, as noted above) and Cro-Magnon 1. However, Murphy (17) systematically examined the frequency of these two trait configurations in a geographically diverse sample of recent human skulls ($n = 206$) and found both the open and roofed-over condition present. The nonroofed (open) condition was argued to be unique to Neandertals by Schwartz and Tattersall (5). However, Murphy (17) found that the open condition was present in all of the subsamples. It was found in an especially high frequency among skulls from the archaeological site of Tepe Hissar, Iran.

## DISCUSSION

There are two distinct issues raised in Schwartz and Tattersall's paper. The first is the issue of Neandertals as a species (*Homo neanderthalensis*) distinct from modern humans (*H. sapiens*) and the degree to which their purported internal nasal autapomorphies lend weight to this taxonomic question. The second issue is the high degree of anatomical difference in Neandertal internal nasal morphology and the attendant differences in respiratory physiology and overall behavior that this difference implies, not only in comparison to modern humans but perhaps to all other terrestrial mammals. In the commentary by Laitman and colleagues (6) on the Schwartz and Tattersall paper and in the references therein, it is argued that these purported autapomorphies (in conjunction with other upper respiratory tract features) are evidence of specialized anatomy, reflecting a variety of adaptive and even maladaptive factors among Neandertals that include, among others, heavier reliance on nasal rather than oral respiration, reduced speech communicatory efficiency, increased risk for serious upper respiratory infections such as chronic sinusitis or middle-ear infections, and a greater proclivity for central or peripheral neuromuscular pathologies.

With respect to the first issue, progress in science works to some degree by consensus, and there is today a greater tendency among paleoanthropologists to view Neandertals as a species distinct from *H. sapiens*. Certainly, not all specialists

in this area concur, but those who do not are increasingly in the minority. A substantial gulf exists between the total craniofacial and postcranial morphological patterns of the Neandertals and modern humans in Europe and western Asia (7, 18). I have little objection to translating these differences to a species-level distinction, especially as a working evolutionary hypothesis. But what might be lost by some proponents of this view in the zeal to make this case is the simple fact that even if Neandertals are a species distinct from *H. sapiens*, they are nonetheless a very closely related species. This point is critical to the second issue. Do we expect major differences in highly functionally constrained anatomical complexes such as the internal respiratory region to arise and be viable at such a low taxonomic level? The remarkable locomotor diversity in extant hominoids might support this expectation, but such differences are still variations at the level of the superfamily, not within a family, and certainly not within a genus.

Although genus-level distinctions are no more objective than any other taxonomic category, evolutionary biologists nonetheless tend to group species into genera based on similarity in their overall adaptive zone or niche and a resultant morphological gestalt or bauplan. Accordingly, although debate regarding the nature of similarity or difference in the locomotor patterns of *Australopithecus* and *Homo* persist, no such debate exists within the genus *Homo*. Broad scale similarity in *Homo* is likely just as true for a functional complex as basic and perhaps even more basic than locomotion: respiratory physiology. Although the specific data presented here do not provide sufficient confirmation of this general principle, I would nonetheless argue that the type of "radical reorganization" of internal nasal anatomy envisaged by Schwartz and Tattersall (5) for the Neandertals is theoretically implausible, and in any case, it can be rejected empirically, given reasonable sampling and appropriate attention to fossil preservation and existing ranges of variation in both fossil samples and recent humans. Therefore, although Neandertals may well constitute a species separate from *H. sapiens* based on other morphological criteria, the purported internal nasal features proffered by Schwartz and Tattersall do not support this contention. Moreover, adaptive and maladaptive speculations for Neandertal upper respiratory anatomy will have to be argued on other anatomical bases.

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